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Morphological Variation and Local Distribution of *Cyprinodon variegatus* in Florida

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TABLE OF CONTENTS

	Page
LIST OF FIGURES	vi
INTRODUCTION	1
Taxonomic and Distributional Review	2
METHODS AND MATERIALS	8
Methods of Counting and Measuring	8
Statistical Methods	12
Material Examined	14
DISTRIBUTIONAL ANALYSIS	19
Distribution of Cyprinodon Populations in Florida	19
Geological Considerations	24
Peninsular Florida	24
South Florida	32
Florida Keys	33
Environmental Considerations	35
Factors Influencing Local Distribution in Florida	39
RESULTS AND DISCUSSION	47
Counts	47
Measurements	56
Sexual Dimorphism	78
Characters of Cyprinodon from Oklawaha Lakes	80
Effects of Environmental Factors on Morphological Variation	83
Geographic Clines	90
Cyprinodon variegatus hubbsi	92
South Florida Race	103
SUMMARY	107

Page

APPENDIX 110

Tables 1-12. Frequency Distribution of Meristic Characters in Florida Cyprinodon 111

Tables 13-31. Proportional Measurements Expressed in Thousandths of Standard Length in Florida Cyprinodon 123

Table 32. Summary of Sexual Dimorphism in Measurements of Florida Cyprinodon 142

Table 33. Chemical Conditions in Oklawaha Lakes . . . 143

Tables 34-44. Morphological Characters of Cyprinodon from Oklawaha Lakes 144

LITERATURE CITED 155

LIST OF FIGURES

FIGURE		Page
1	Distribution of Cyprinodon in Florida	21
2	Lateral Scales in Florida Cyprinodon	49
3	Circumference Scales in Florida Cyprinodon	51
4	Belly Scales in Florida Cyprinodon	54
5	Proportional Measurement of Body Depth Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	57
6	Proportional Measurement of Body Depth Expressed as Thousandths of Standard Length in Male Florida Cyprinodon	58
7	Proportional Measurement of Body Width Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	60
8	Proportional Measurement of Caudal Peduncle Depth Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	61
9	Proportional Measurement of Predorsal Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	63
10	Proportional Measurement of Dorsal Origin to Caudal Base Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	64
11	Proportional Measurement of Anal Origin to Caudal Base Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	65
12	Proportional Measurement of Anal Origin to Caudal Base Expressed as Thousandths of Standard Length in Male Florida Cyprinodon	66

FIGURE		Page
13	Proportional Measurement of Pelvic Fin Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	68
14	Proportional Measurement of Head Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	69
15	Proportional Measurement of Head Depth Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	71
16	Proportional Measurement of Head Depth Expressed as Thousandths of Standard Length in Male Florida Cyprinodon	72
17	Proportional Measurement of Postorbital Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	73
18	Proportional Measurement of Interorbital Bony Width Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	75
19	Proportional Measurement of Orbit Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	76
20	Proportional Measurement of Orbit to Angle of Preopercle Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	77
21	Proportional Measurement of Opercle Length Expressed as Thousandths of Standard Length in Female Florida Cyprinodon	79
22	Proportional Measurement of Anal Origin to Caudal Base Divided by Body Depth in Female Florida Cyprinodon	99
23	Proportional Measurement of Anal Origin to Caudal Base Divided by Body Depth in Male Florida Cyprinodon	100

INTRODUCTION

There has been much work in recent years on the systematics and evolution of Cyprinodon species (pupfish) from western North America (Miller, 1943a,b, 1948; LaBounty, 1968; and LaBounty and Deacon, (1972), while the status of Cyprinodon variegatus Lacepede and C. hubbsi Carr (1936a) from the east have been neglected. The purpose of this study was to investigate the morphological variation and systematic relationship of C. variegatus and C. hubbsi in Florida.

Since hubbsi was first described (Carr, 1936a), its status as a valid species and relationship to variegatus have been in question (Hubbs and Miller, 1942; Christensen, 1965). The range of hubbsi is limited to the headwaters of the Oklawaha River in central Florida. Because the ecological requirements of C. hubbsi are very narrow (McLane, 1955), and the quality of the lakes which it inhabits has declined radically in recent years (Brezonik et al., 1969), there has been concern for its survival.

The subspecies C. v. variegatus is known to occur along most of the coast of Florida, at times penetrating into fresh waters. A second subspecies, C. v. riverendi Poey, originally described from Cuba, has been thought to exist in the Florida Keys (Jordan and Evermann, 1896; Fowler, 1906; and Hubbs, 1936). Within the range of C. variegatus in Florida, wide morphological variation has been

noted (Carr, 1936a; Hubbs, 1936; Raney et al., 1953; and McLane, 1955), and the presence of other well-defined taxonomic units has been postulated (Hubbs, 1936; and Raney et al., 1953).

Taxonomic and Distributional Review

Briggs (1958) gave the distribution of Cyprinodon variegatus as Cape Cod to the southern tip of Florida and west along the Gulf coast to Mexico. Within this range Hubbs (1936) recognized three subspecies: ovinus (Mitchell) which occurs from Massachusetts to Virginia, variegatus Lacepede from North Carolina to Brownsville, Texas and into Mexico, and artifrons Hubbs in the Yucatan peninsula of Mexico. A fourth form, the Cuban C. v. riverendi (Poey) was tentatively recognized in southern Florida. More recently the distribution of C. variegatus has been extended by introduction into Washington (Greenfield and Grinols, 1965).

The Yucatan subspecies C. v. artifrons is characterized by the retention of the black spot on the dorsal fin of males, a characteristic present in the females of C. v. variegatus. This spot is sometimes bordered anteriorly by an incomplete pale margin in the mature artifrons male (Hubbs, 1936). There are striking differences between the body form and proportions of artifrons and ovinus. Hubbs (1936) stated that there can be little question as to the validity of these differences. C. v. variegatus is intermediate between artifrons and ovinus in virtually all features of body form and of fin shape which separate these subspecies. Because of the intermediacy of these three forms, they are regarded as only subspecifically distinct (Hubbs, 1936).

C. v. riverendi from Cuba was described as having scales larger than variegatus (Hubbs, 1936). Hubbs (1936) stated that these larger scales are present in specimens from Jamaica but not in specimens from the Florida Keys, referred to as riverendi. C. v. riverendi was described as similar to C. v. variegatus except that they were more arched on the nape and more pot-bellied.

Many closely related West Indian species of Cyprinodon have been described since 1868. Poey described the Cuban species Cyprinodon felicianus in 1868. Myers (1935) stated that this species was described from a single specimen and that the species was very close in morphological appearance to C. v. riverendi. Meek described C. dearborni from the Dutch West Indies and Venezuela in 1909. In 1932 C. baconi was described from Lake Forsyth, Andros Island, Bahamas (Breder, 1932). Breder (1932) stated that this species was clearly distinct from any then known but belonged to the variegatus-riverendi-dearborni group on the basis of its enlarged humeral scale and color pattern. Myers (1935) described C. bondi from Hispaniola. This species was thought to be unique because of a high lateral scale count (28-30) and the lack of an enlarged humeral scale in the adult. Fowler (1939) reported a new species, C. jamaicensis, from Jamaica. In 1942, Hubbs and Miller (1942), described the species C. laciniatus from the Bahamas. This species is characterized by strongly laciniated scale margins. Hubbs and Miller (1942) expressed the idea that this species could possibly be separated at the generic level.

The taxonomic status of most of these nominal forms is uncertain. Hubbs and Miller (1942) pointed out that all West Indian species of

Cyprinodon are very similar to C. variegatus and might eventually be treated as its subspecies. Miller (1962) confirmed his earlier suspicions that C. baconi was a synonym of C. variegatus. Miller speculated that future examination would confirm baconi as a valid subspecies of variegatus. The status of the other West Indian forms seems uncertain although C. bondi and C. laciniatus seem to stand out from the C. variegatus complex (Miller, 1962). Bohlke and Chaplin (1968) stated that Cyprinodon variegatus is known from the Bahamas, but that its range in the West Indies is unknown because of the inadequate knowledge of Cyprinodon species in that area.

Other variations within Cyprinodon variegatus have also been noted by many investigators. Carr (1936a) found that variegatus from the west coast of Florida showed a greater enlargement of the humeral scale and more scale rows on the belly, among other differences, than specimens from the east coast of Florida. Raney et al., (1953) noted that territorial holdings and behavior of individuals of Cyprinodon from Everglades, Florida, were somewhat different from those from a small freshwater stream near Alva, Florida. These differences in behavior were attributed to differences in the available spawning ground in proportion to the abundance of breeding males present and were probably not genetic. Intraspecific variation in the osmotic abilities of C. variegatus from the Texas coast have been demonstrated. Results showed that "genetic differences were small and that environmental factors may be more important in producing variations in these abilities than simple genetic factors," (Martin, 1968:1188).

Cyprinodon variegatus from isolated freshwater populations in the St. Johns River show indications of limited differentiation (McLane, 1955). One population, at Green Springs on Lake Monroe, showed differentiation in the ecological niche inhabited. In this spring, variegatus were reported to inhabit areas where the bottom consisted of flocculent organic matter about twelve inches deep and not the firm sand bottom habitats characteristic of the species elsewhere in the St. Johns system (McLane, 1955). I made collections in this same spring but did not collect C. variegatus.

While conducting a study of the morphological differences between C. variegatus and laciniatus, Gilmore and Williams (unpublished manuscript) noted morphological variation among some populations of C. variegatus from along the east coast of Florida. Collections from the Indian River were so variable that they were postulated to be divergent forms of variegatus, superficially similar to C. laciniatus.

In 1936 Cyprinodon hubbsi was described from Lake Eustis, Florida (Carr, 1936a). Subsequently it was reported from most of the major lakes of the headwaters of the Oklawaha River (Reid, 1948; Hellman, 1954). Carr (1936a:160) stated that "although apparently closely allied to the subspecies of C. variegatus, the several unique characters of this form, and the fact that it is isolated in a body of freshwater whose connection with the Atlantic is 200 miles in length, led me to believe that it should be accorded specific rank."

Carr (1936a) differentiated hubbsi from variegatus on the basis of the following features: 1) reduced pigmentation, 2) less elevated contour at the dorsal origin (lesser body depth), 3) lesser interorbital width, 4) eleven anal rays, and 5) smaller size.

Cyprinodon variegatus from the west coast of Florida was said to show a greater enlargement of the humeral scale and more scale rows on the belly than variegatus from the east coast. In these respects hubbsi was deemed to be more closely allied with the west coast variegatus (Carr, 1936a). Although it was quite similar to Cyprinodon variegatus, Carr stated that he could not place hubbsi in the subspecies gradient, ovinus-variegatus-artifrons, described by Hubbs (1936). Miller (1942) noted that C. hubbsi was among species very similar to C. variegatus, and that the former might eventually be treated as a subspecies of variegatus. Liu (1969) states that Miller (personal correspondence) had concluded that hubbsi, jamaicensis, dearborni, and subspecies of variegatus should be synonymized.

Christensen (1965) expanded the range of hubbsi from the headwaters of the Oklawaha River to include areas of fresh water from Palm Beach to Dade County. Cyprinodon variegatus is not known to occur in the coastal regions of this area from Palm Beach and Broward Counties.

Christensen (1965:69) stated that south Florida populations of hubbsi are "generally more robust than those taken in the typical lake habitat and somewhat deeper bodied than those described by Carr (1936a). I have since seen specimens of comparable size in recent collections from Lake Eustis and Lake Dora." In this statement Christensen described morphological characters which are more characteristic of coastal C. variegatus than hubbsi. This does, however, indicate that the description of hubbsi by Carr (1936a) was inadequate. Christensen (1965) noted that many of the specimens

recently collected from Lake Eustis exceeded the ranges of variation given by Carr and were similar to many of his specimens from Palm Beach County.

There has been some evidence that the breeding colors and courtship behavior of hubbsi are distinct from variegatus. These ideas are based upon an M.S. thesis investigation conducted by Robert Steinbach at Florida State University. The thesis was never completed and no notes or details can be recovered (personal correspondence, R. W. Yerger to F. F. Snelson). In limited observations I have been unable to document any such differences. I did note that hubbsi has considerable ability to change pigmentation shading depending upon the habitat coloration. This ability could lead to inaccurate assumptions as to the pigmentation variation among populations. Specimens of hubbsi are consistently much lighter in coloration since they all inhabit areas of lakes with clean, white, sand bottoms. Liu (1969) has speculated that large genetic differences do not exist among most forms of Cyprinodon, since he was able to produce F_1 hybrids in the majority of the species crossed. Lack of variation was found to be particularly evident within superspecies behavioral groups when considering courtship behavior and species recognition. Courtship behavior was found to be relatively unimportant in mating and a low degree of species recognition was noted among various forms of Cyprinodon (Liu, 1969; and Stevenson and Buchanan, 1973).

METHODS AND MATERIALS

Methods of Counting and Measuring

Methods of measuring and counting morphological characters used in this study followed Miller (1948) and Hubbs and Lagler (1964) except as noted below. Measurements were made under a steromicroscope with a Helios dial caliper to an accuracy of 0.01 mm. Measurements and counts were obtained from the left side of the fish unless otherwise stated. Occasionally it was necessary to measure a structure or to make a count on the right side due to an injury on the left side. Deformed fish or fish with damaged fins were not selected for measuring. Whenever possible, those fish with open or protruding mouths were not chosen due to the difficulty in closing the mouth to a normal position for measuring to the tip of the premaxillaries.

Because morphometric and secondary sexual characteristics may exhibit seasonal variation, attempts were made to measure specimens collected during the same time of the year (summer). Morphometric data may also vary allometrically with growth and thus specimens from a limited size range were selected. All counts and measurements used in statistical comparisons were based on specimens 27-41 mm Standard Length (SL). The minimum value was chosen because female *C. variegatus* have been found to mature at 27 mm SL (males are mature at 24 mm SL) (Warlen, 1964). The maximum value was the SL of the largest specimen

of C. hubbsi obtained (41.2 SL). Thus all fishes examined in this study were within the size range known for C. hubbsi.

Explanation of certain procedures employed in counting and measuring which differ from Miller (1948) and Hubbs and Lagler (1964) or were originated in this investigation follow:

Predorsal Scales. The predorsal count involves the scale rows which intercept the mid-line running from the occiput to the origin of the dorsal fin. When necessary, the mid-line was shifted to the side when an otherwise obviously incorrect count would result.

Dorsal Origin to Belly Mid-Line. This count begins with the scale just beside, but not anterior to, the origin of the dorsal fin and continues along a straight scale row passing usually one scale posterior to the humeral shield and under the pectoral fin, to and including the scale along the mid-line of the belly. This scale count is a modification of the opercle to dorsal scale count of Chipman (1958).

Belly Scales. The belly scale count begins with the first scale on the belly mid-line in the isthmus and continues posteriorly along the mid-line to and including the scale between the pelvics or the first scale for which more than one-half of its exposed surface lies posterior to the origin of the pelvics. Scales which meet at the mid-line are counted as one.

Suborbital Scales. This scale count begins with the uppermost scale on the preopercle directly posterior to the orbit and continues along the lower edge of the orbit to and including the uppermost scale in the preorbital region. Where a choice is involved, the scale

nearest the orbit is chosen provided a continuous count can be made along scales whose exposed surfaces are in contact with one another. A jet of air is often needed to dry the scales in order to see them in the preorbital region.

Scales of the Preorbital Region. Scales in the preorbital region were described by three methods, all of which attempt to determine the upper level to which the preorbital area is scaled. The first involves coding the height to which the uppermost scale reaches in relation to the lachrymal pores. When a full compliment of pores is present, the lowest equals one and the highest equals four. The height was then estimated to tenths between pores. If the preorbital region was scaled to a level halfway between the third and fourth lacrymal pore, this would be coded as 3.5. The second method determines the upper level in relation to the nostrils. If the preorbital region was scaled below or to the level of the nostril, this was coded as two and if scaled above the nostril, this was coded as one. The third method determined the level in relation to the middle of the orbit. If scaled below the level of the middle of the pupil, this was coded as two and if equal to or above this level, a code of one was used.

Caudal Peduncle Scales. This scale count was made in a zigzag fashion around the caudal peduncle beginning with the third scale from the last in the lateral series.

Frontal Scales. The frontal scale count involves the scales which lie on the mid-line of the head between the snout and the occiput. The first scales may be a pair of two smaller scales lying side by side on the snout. If the exposed surfaces of these scales overlapped

at the mid-line of the snout, they were counted as one-half; if they did not overlap or were merely two small scales at the corner of the next scale, they were omitted from the count. The basic pattern of the Cyprinodon frontal scalation pattern is described by Hoedeman (1958), although he includes one scale posterior to the occiput in his pattern. In my count the second scale anterior to the occiput is usually enlarged and nonimbricated and lies partially over and partially behind the posterior rim of the orbit and overlaps both the scales anterior and posterior.

Head Pores. The head pores were counted on the left side as described by Gosline (1949) and Miller (1948) for Cyprinodon.

Body Depth. This is the greatest vertical dimension between the back and the ventral surface of the abdomen. It was measured from the dorsal fin origin to the ventral surface between the pelvics.

Body Width. This measurement is the greatest horizontal distance between the sides of the body, measured over the back immediately posterior to the humeral shield. At this point the measurement is not affected by the distended abdomen of spawning females (Chipman, 1958).

Pectoral Origin to Dorsal Origin. This measurement is the distance from the structural base of the first dorsal ray to the structural base of the first pectoral ray. This method was created in order that a depth measurement might be made which is not influenced by the distended abdomen of a gravid female.

Height of Cheek. It is the least distance from the orbital rim to the lower edge of the anterior arm of the preopercle.

Length of Cheek. This character is measured from the border of the lachrymal at the corner of the mouth to the pre-opercular angle.

Interorbital Bony Width. This measurement is the least distance between the bony rims of the orbits (measured above the middle of the pupils). The caliper points are pressed firmly against the bony rims on each side.

Length of Orbit. This character is the greatest horizontal distance across the fleshy orbital rims. This measurement is done slightly oblique (higher posterior and lower anterior from the horizontal) where the distance is greatest and the posterior fleshy rim is tightly against the bony rim.

Orbit to Angle of Preopercle. This measurement is the distance from the orbit to the angle of the preopercle.

Statistical Methods

Morphometric data were taken on both males and females and were expressed in thousandths of standard length. Most characters are discussed individually to permit comparisons of trends among various populations. For each character the mean, limits of variation, clinal trends, and possible correlations with salinity are given. No differences between sexes were noted for the meristic data, therefore, data on males and females were grouped together for analysis. Meristic and morphometric data for hubbsi are given separately for each lake.

To avoid confusion due to sexual dimorphism or to morphometric characters where growth may be allometric in only one sex, all data presentations and statistical comparisons are independent for each sex. Because larger sample sizes were available for females, most graphical analysis was based on that sex. Bar graphs are presented for morphometric character which showed any geographical trend among populations.

In all cases the data from males, presented in the tables, corresponds closely to that presented graphically for females. In a few instances graphs are drawn for males when a particular character was of value for separation of hubbsi from other Cyprinodon populations. Few male specimens were available from collections from fresh waters of Dade County (FDAD), accounting for the absence of appropriate data in Tables 13 through 34.

All data were punched on cards and run on an IBM 360/65 computer at Florida Technological University. The statistical analyses were performed with the Statistical Package for Social Sciences (SPSS) containing one-way analysis of variance, subprograms Oneway and Crosstabs, and revised MANOVA program for analysis of variance and covariance. Subprogram Crosstabs was used for a display breakdown of meristic data and the subprogram Oneway was used not only for analysis of variance, but also to calculate a mean, standard deviation, standard error, maximum and minimum values, and 90 per cent confidence interval for all characters in each population studied.

Analysis of variance was performed on all meristic characters, while morphometric characters were subjected to analysis of covariance with standard length as the covariate in each case according to Vandermeer (1966). Since the measurements increase with the length of the fish, an adjustment was necessary to compensate for variation in the size of individuals. The body measurement of sample means were adjusted to a common length by analysis of covariance, and the regression on standard length was determined for each character. The Student-Newman-Keules (SNK) test was used as needed for multiple

comparison tests to determine which samples are significantly different (Vandermeer, 1966).

This study was begun with a preliminary investigation of suspected extreme populations using many characters. Appropriate analyses were performed on the preliminary data to determine which characters were of most use in distinguishing variation among populations. The following characters proved to be of no value in differentiating populations and were dropped from further investigation: pectoral rays, pelvic rays, cheek scales, caudal peduncle scales, head pores, prepelvic length, dorsal fin length, anal fin length, pectoral fin length, caudal fin length, head width, cheek length, mouth width, upper jaw length, and preorbital width.

Upon completion of the taking of data, the student's t test was used on morphometric characters to determine which characters showed significant sexual dimorphism. Meristic data were analyzed by analysis of variance and morphometric data by covariance to determine if population means were unequal for each character. For all morphometric data, the means were shown to be significantly different among the various populations. Further evaluations were made by visual inspection of data graphs and plots along with the SNK multiple comparison test as deemed appropriate.

Material Examined

Populations of Cyprinodon used in this study and listed in the tables and figures are labled with codes of three or four letters. The explanation of these codes and the collections contained within

each are included in the descriptions below. Collections are recorded by museum number, state, county and location. Materials identified for use as distributional data are not included. Abbreviations of institutions from which examined materials are deposited are as follows: Florida Technological University (FTU), Florida State University (FSU), University of Florida (UF), Cornell University (CU), Jacksonville University (JU), and Florida State Board of Conservation Marine Laboratory (FSBC). Further abbreviations included in explanations of materials examined, other than those which are standardly accepted, are as follows: county = co., highway = hwy., route = rt., miles = mi., junction = jct., road = rd.

HUBB = Cyprinodon hubbsi, fresh waters at headwaters of Oklawaha River, Lake and Marion Counties. Florida, Lake Co.: FSU 18011 (Lake Harris, 1.0 mi. E. Leesburg on Rt. 27), FTU WEJ-73-20 (Lake Harris, Silver Glenn Springs), FSU 18183 (Lake Eustis, Eustis Community Center), JU 1355 (Lake Yale), JU 199 (Lake Dora, at Mt. Dora), FSU 18113 (Lake Dora, Tavares boat ramp), FSU 15147 (Lake Griffin, 5 mi. N. Leesburg on S-466A), Marion Co.: FSU 18003 (Lake Weir, Eaton's Beach, S. side of lake), JU 1349 (Lake Weir).

ESCA = Escambia Co., coastal estuarine areas. Florida, Escambia Co.: FSU 14299 (Santa Rosa Island, ditch N. Hwy. 399).

OKAL = Okaloosa Co., coastal estuarine areas. Florida, Okaloosa Co.: FSU 1929 (Turkey Creek, W. edge of Niceville).

WALT = Walton Co., coastal estuarine areas. Florida, Walton Co.: FSU 16883 (Grayton Beach State Park, tidal pool).

GULF = Gulf Co., coastal estuarine areas. Florida, Gulf Co.: FSU 12415 (Indian River Pass Beach, 0.1 mi. S. Rt. 30 on Rt. 30-B).

TAYL = Taylor Co., coastal estuarine areas. Florida, Taylor Co.: FSU 15734 (Adams Beach, 5 mi. W. Keaton Beach).

LEVY = Levy Co., coastal estuarine areas. Florida, Levy Co.: UF 780 (Cedar Key, borrow pit S. side of airstrip), UF Kilby 7-2448-2 (Cedar Key, culvert pool).

HERN = Hernando Co., coastal estuarine areas. Florida, Hernando Co.: UF 3082 (Bayport, Palm Point), UF Kilby 2-2848-5 (Bayport, W. sandhill ditch).

PINE = Pinellas Co., coastal estuarine areas. Florida, Pinellas Co.: FSBC 413 (Old Tampa Bay, flats S. Big Island), CU 47145 (Bayou, S.E. side Cross Bayou Canal at Rt. 694), FSBC 576 (Tampa Bay, Beach Drive at 15th Ave. S.).

SARA = Sarasota Co., coastal estuarine areas. Florida, Sarasota Co.: CU 43778 (stream E. of Rt. 41, 10 mi. S. of Rt. 60), UF 4018 (Sarasota Pass).

LEE = Lee Co., coastal estuarine areas. Florida, Lee Co.: FTU FFS-71-11 (Sanibel Island, dirt rd. W. of Tarpon Bay).

ALVA = Alva, fresh waters of Caloosahatchee River near Alva. Florida, Lee Co.: CU 21949 (tributary at E. limits of Alva on Rt. 80).

FLAM = Flamingo, coastal estuarine areas near Flamingo, Everglades National Park. Florida, Monroe Co.: CU 22058 (Flamingo, Everglades National Park), CU 15939 (Slage's Ditch, 6 mi. W. of Flamingo).

FDAD = Dade Co., fresh waters in southern Dade Co. Florida, Dade Co.: JU 439 (Lake Chekika Mineral Springs), UF 5099 (borrow pit 2 mi. W. of Florida City).

LARG = Key Largo and Cross Key, coastal areas. Florida, Monroe Co.: FSU 16603 (Key Largo, Pennecamp State Park), JU 872 (Cross Key, U.S. 1 at Aeojet Canal), JU 192 (Cross Key).

LMAT = Lower Matecumbe Key and surrounding coastal areas. Florida, Monroe Co.: CU 10243 (Lower Matecumbe Key).

BIGP = Big Pine Key and surrounding coastal areas. Florida, Monroe Co.: CU 23627 (Big Pine Key, Long Beach), CU 48991 (Bahia Honda Key, lagoon mouth, 1 mi. E. State Park), JU 941 (Big Pine Key).

PALM = Palm Beach Co., fresh water areas. Florida, Palm Beach Co.: FSU-10490 (ditch along Indian Town Rd., Rt. 706, 11 mi. W. of Jupiter), FSU 12653 (ditch along Indian Town Rd., Rt. 706, 11 mi. W. of Jupiter).

OKEE = Lake Okeechobee, fresh water. Florida, Martin Co.: JU 1334 (Lake Okeechobee, 3 mi. S. Treasure Island on Rt. 441).

INDI = Indian River Co., coastal estuarine areas. Florida, Indian River Co.: CU 4949 (0.8 mi. E. jct. U.S. 1 and Rt. 606).

SBRE = South Brevard Co., coastal estuarine areas of the southern parts of the county. Florida, Brevard Co.: CU 49173 (7.7 mi. S. of jct. U.S. 1 and Rt. 514 near Grant).

MERR = Merritt Island, coastal and estuarine areas. Florida, Brevard Co.: FTU KSC-F-64 (impoundment 200 yards N. of vehicle assembly building along Rt. 3), JU 894 (Indian River at Rt. 1, Titusville, 3.6 mi. S. jct. Rt. 402).

HARN = Lake Harney, St. Johns River, fresh waters. Florida, Seminole Co.: FTU RLH-71-09 (Lake Harney, end of Lake Harney Rd.), Volusia Co.: FTU (E. shore of Lake Harney).

VOLU = Volusia Co., coastal estuarine areas. Florida, Volusia Co.: JU 804 (1.5 mi. S. Flagler Co. line, Rt. 201), JU 811 (Tomoka River State Park).

STJO = St. Johns Co., coastal estuarine areas. Florida, St. Johns Co.: FSU 10430 (Anastasia State Park, Anastasia Island).

DUVL = Duval Co., coastal estuarine areas. Florida, Duval Co.: FSU 13866 (St. Johns River, 1 mi. upstream, 0.5 mi. S. Mayport).

NASS = Nassau Co., coastal estuarine areas. Florida, Nassau Co.: JU 112 (S. end Amelia Island at Buccaneer Rd.), UF 5228 (tidal creek near O'Neil on Rt. 108).

Throughout this paper collections are arranged in geographical order beginning with Escambia County in the western panhandle of Florida, proceeding southward along the west coast to the Florida Keys; from this point collections are arranged in geographical order as they occur proceeding north along the east coast. Populations are usually arranged according to counties, however, some collections from freshwater areas are arranged in the geographical sequence which would occur at the nearest coast line or at the point in the sequence at which geological data indicates a place of probable origin of the population. Some areas (groupings) were occasionally combined to obtain larger sample sizes. These combinations did not change any clinal trends or overall results. The group of hubbsi specimens is arbitrarily placed at the beginning of the order because of the central location of the headwaters of the Oklawaha River in the state.

DISTRIBUTIONAL ANALYSIS

Distribution of Cyprinodon Populations in Florida

Cyprinodon variegatus is a coastal species found in relatively shallow brackish or nearby fresh water where the bottom is at least partially sandy and little wave action is present (Fanara, 1964). The species occasionally penetrates many miles up freshwater rivers (Martin, 1969) and may establish permanent breeding populations in freshwater lakes. The Florida coast provides ideal habitat for the species, especially in the inlets, brackish water estuaries, and lagoons protected by barrier islands.

The east coast of Florida from Georgia to Miami Beach consists of a series of sandy barrier islands, broken occasionally by inlets. The series of lagoons behind these islands form the Intracoastal Waterway. South of Miami, through the Florida Keys to Cape Romano, the coast is bordered by shallow waters, intricate mangrove swamps, and few sandy beaches. Between Cape Romano and Anclote Keys, north of Tampa, the outer shore of the Gulf of Mexico is composed of barrier islands like those of the east coast. From the Anclote Keys to the mouth of the Ochlockonee River there are no barrier islands; this shore is intricate, composed of scattered mangrove swamps. At the Ochlockonee River, beach ridges and barrier islands once again border the coast and extend to the Mississippi Delta (Cooke, 1939).

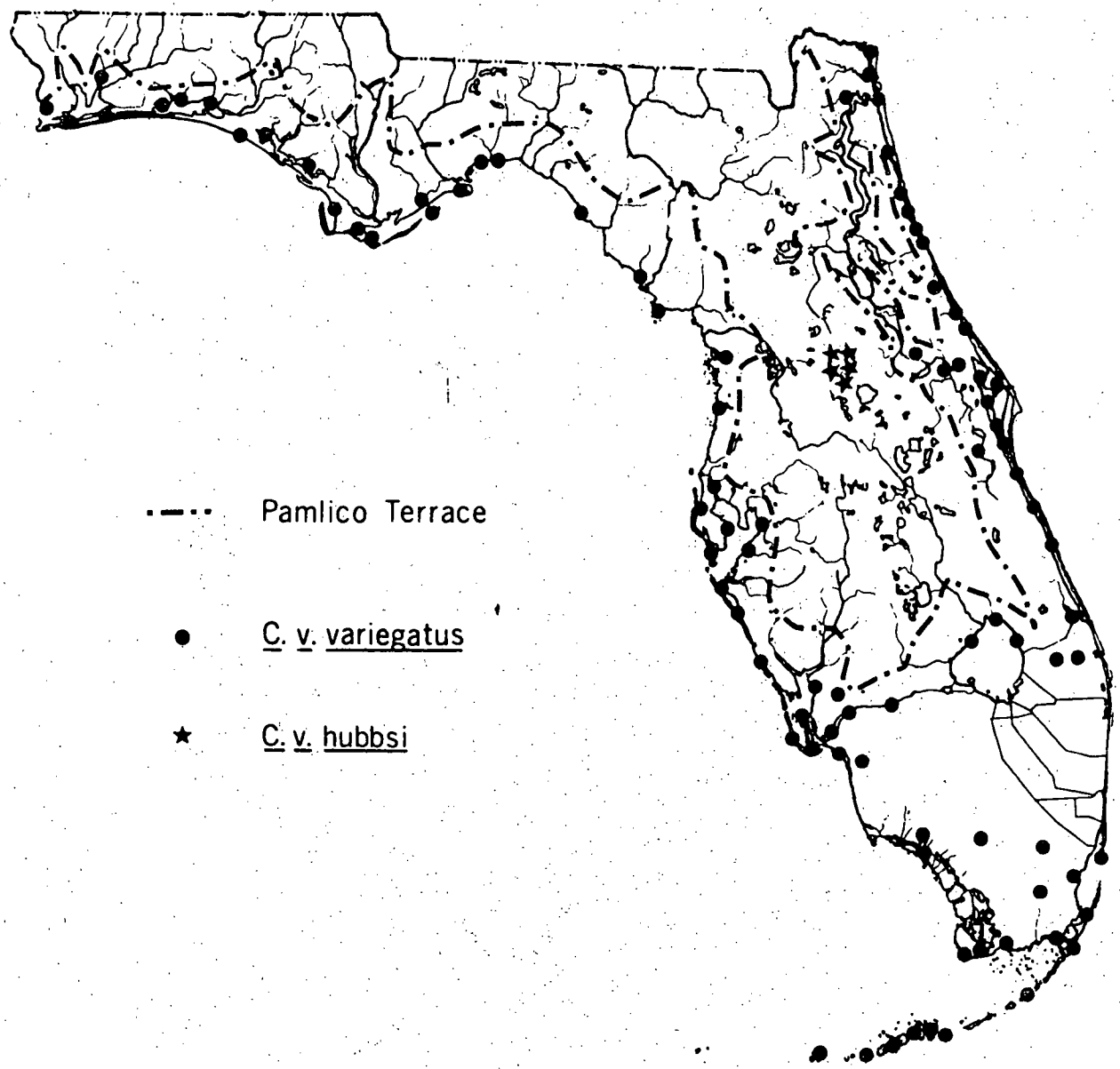
The local distribution of Cyprinodon variegatus is well known since many collections have been made in brackish and coastal waters of Florida. The distribution of Cyprinodon in Florida is shown in Figure 1.

Cyprinodon variegatus appears to inhabit the entire east coast marsh and lagoon areas of Florida from Nassau County to the Palm Beach County. From the St. Lucie Inlet, south through the Jupiter area, no Cyprinodon variegatus have been found. Gunter and Hall (1963) found no variegatus in the brackish waters of the St. Lucie estuaries, although one specimen was found a few miles west, in the fresh waters of the St. Lucie Canal. Christensen (1965) also noted that no C. variegatus were known to occur in the coastal marshes of the Jupiter area. The reason for the apparent absence of variegatus from these waters is unknown, although an unusual geological condition in this area will be described later. A general lack of all cyprinodontids from this area south through the vicinity of Biscayne Bay has been noted by Relyea (personal communications). Christensen (1965) stated that Fundulus grandis was the only cyprinodontid found in the Jupiter coastal areas. Gunter (1956:618) noted that a peculiarity of the Louisiana marsh area is the "virtual absence of cyprinodontid fishes over the general expanse." Thus it appears that ecological conditions exist in some coastal marsh areas which tend to exclude cyprinodontids.

Gore (1972) has stated that the central east coast of Florida is considered a transitional zone between the Tropical Antillean faunal province and the warm temperate Carolinian faunal province. This zone is reported to have its southern boundary near Jupiter Inlet and northern

FIGURE 1

Distribution of Cyprinodon in Florida.


Pamlico Terrace
C. v. variegatus
C. v. hubbsi

boundary around the Cape Canaveral area. Narrow barrier islands separate the Indian River lagoon from the sea along the entire coast of this zone. Work (1969) found that the West Indian molluscan fauna had its northern most range, and the Carolinian fauna its southernmost range in this same general area, more specifically the St. Lucie Inlet near Stuart, Florida.

Cyprinodon variegatus reappears on the east coast in the coastal waters of Biscayne Bay. Its range extends throughout the coastal marsh areas of south Florida and the Keys. The Cuban subspecies, Cyprinodon variegatus riverendi has been reported from the Florida Keys by Jordan (1884) and Jordan and Evermann (1896). Fowler (1906) reported the subspecies from Boca Chica Key and from the Marquesas Keys.

C. variegatus appears to be uniformly distributed along the entire west coast of Florida. Disjunction may occur only in the area from the Anclote Keys to the Ochlocknee River, where populations may be more isolated due to the absence of barrier islands and thus a reduction of suitable habitat.

Freshwater populations of C. variegatus are also present in Florida. Some collections in fresh waters have resulted from the penetration of variegatus into rivers, while others are permanent, breeding populations. McLane (1955) collected variegatus from permanent populations in regions of the St. Johns River where the waters have unusually high salt concentrations. This region, from Lake Winder to Lake Harney has salinities varying from 0.028 ppt to 10.70 ppt.

McLane (1955) also noted a small population of variegatus in the Green Spring Run on Lake Monroe.

A specimen of variegatus was observed in the waters of Homosassa Springs in west Florida (Citrus County), but this specimen was not captured (Herald, 1949). Ager (1971) collected variegatus from the fresh waters of Lake Okeechobee. Lake Okeechobee drains to the east through the St. Lucie Canal, into the St. Lucie estuary and the Atlantic. Gunter and Hall (1963) collected one specimen from this estuary where the waters are essentially fresh. To the west, Lake Okeechobee drains through the Caloosahatchee River, into the Gulf of Mexico. Raney et al., (1953) studied the reproductive behavior of variegatus from this river near Alva, Florida, and Gunter and Hall (1965) made collections of the species from fresh waters near the mouth of the river.

In southern Florida, Martin (1969) collected variegatus from a freshwater canal about seven miles north of Homestead, Florida, and Kilby and Caldwell (1955) collected the species from a borrow pit along Highway 27 about three miles southwest from this city. Christensen (1965, and personal communications) has collected Cyprinodon in fresh waters of south Florida from Palm Beach County to the Loop Road off the Tamiami Trail. It appears that Cyprinodon may occur throughout the fresh waters of the Everglades in south Florida.

Carr (1936a) described Cyprinodon hubbsi from Lake Eustis, Florida, and noted that although he had done extensive seining in similar habitats in several neighboring lakes, including Lake Harris, no hubbsi were taken outside Lake Eustis. Reid (1949) extended the

range of C. hubbsi to include Lake Weir, a lake approximately eighteen miles northwest of Lake Eustis. Lake Weir is connected to the Oklawaha River, and thus Lake Eustis, by a drainage canal which was constructed in the 1950's. Spillways present in the canal probably prevent the movement of fishes through the canal (Reid, 1949). Hellman (1954) extended the range of hubbsi to include Lakes Harris, Griffin, and Dora. All of these lakes are interconnected with Lake Eustis to form the major headwaters of the Oklawaha River, a tributary to the St. Johns River. Subsequent collections and examination of museum specimens by myself have expanded the range of hubbsi to Silver Lake and Lake Yale.

Christensen (1965) further extended the range of Cyprinodon hubbsi to include Palm Beach County. Specimens identified as hubbsi were taken from at least six freshwater localities widely distributed in Palm Beach County. Christensen speculated that this wide distribution indicated that hubbsi was not a recent introduction. Christensen (personal communications) later expanded this range to include areas as far south as the Loop Road off of the Tamiami Trail.

Geological Considerations

Peninsular Florida. The area of land and water on the Florida Plateau has varied greatly during the millions of years it has been in existence. During this time, the sea fluctuated between levels above and below the present sea level. Ocean levels were lower because of water bound in glacial ice, and correspondingly higher during glacial retreat. When the water remained high for relatively long periods of time, waves and currents eroded the sea floor to form level terraces.

A level plain and an abandoned shoreline were produced when the sea level later dropped. Sand dunes were then built up along new shorelines. These changes of sea level left their marks not only on Florida, but on coastal regions everywhere (Cooke, 1939).

The formation of the marine terraces was not a continuous process of the sea level dropping from the level of one terrace to the next lower terrace. Between the formation of these terraces the sea level may have dropped to as much as 200 feet below the present sea level and then recovered to the height of the next lower terrace (Cooke, 1939). Johnson (1972:186) states that "the shore extended much farther out on the continental shelf as little as 11,000 years ago."

The Penholoway terrace is the highest shore line in Florida to directly affect the present day distribution of Cyprinodon. This terrace existed when the sea was 70 feet higher than the present level (Cooke, 1939). Cooke postulated this terrace to be the result of a drop in the sea level during the Sangamon interglacial period. Minor physiographic evidence is present for the existence of this insignificant stand of sea level at elevations of 70 to 80 feet (Alt and Brooks, 1965). When the sea dropped from the previous Wicomico terrace to the 70 foot level, the Wicomico islands were allowed to fuse into a long, narrow peninsula which extended southward to about the Highlands-Glades county line and was connected with the mainland in the north. This allowed the gradual formation of extensive freshwater areas which proved attractive to continental freshwater organisms (Cooke, 1939; and Briggs, 1958). Alt and Brooks (1965) date this 70 to 80 foot terrace at Late Pliocene or Early Pleistocene. Until recently it was believed

that peninsular Florida was separated from the rest of the southeastern United States during each interglacial period. The evidence of Alt and Brooks dates the last unquestionable complete separation of peninsular Florida as Late Pliocene. This separation existed in the area of the present day Suwannee River Valley and was called the "Suwanne Straits" (Cooke, 1939; and Gilbert and Bailey, 1972).

In central Florida the Penholoway shore formed a four to six mile wide terrace along the border of the Withlacoochee River as far west as Dunnellon and as far east as Wildwood. This terrace may have formed the bottom of an estuary or lakes during Penholoway time. Several of these large basins occur in Marion County and one in particular existed along what is now the Oklawaha River. Innumerable shallow lakes were formed during this time in Lake County along with larger, deeper, open lakes such as Lake Apopka and Lake Harris which now form part of the headwaters of the Oklawaha River (Cooke, 1945). Carr (1936b) postulated that C. hubbsi was a marine relict of these sea floor depressions or lagoons since there is a poorly developed direct drainage connection between the headwaters of the Oklawaha and the Atlantic. Thus migration of this species through these waters seems improbable.

The Talbot terrace, another insignificant stand, is found at about 42 feet above sea level (Cooke, 1945). This terrace was previously dated at the Pleistocene Sangamon interglacial (Cooke, 1945) but is now thought to have been formed during the Aftonian interglacial period when the sea rose to 45-50' feet above the present sea level (Alt and Brooks, 1965). The Talbot terrace extended the peninsula south to about Highlands County and east to about what is now the St. Johns

River. One large island extended southward 12 miles from the present eastward course of the St. Johns River, passing four miles east of Jacksonville (Cooke, 1939). With the formation of the Talbot terrace, the estuary which was postulated to exist in the Oklawaha River now extended southward only through Marion County to near the Lake County line. Thus, by this time the large lakes now inhabited by hubbsi in Lake County were probably isolated from the rest of the estuary.

The Pamlico shore line is the best preserved of the Pleistocene shores. This terrace was formed when the sea rose to a level of 25 feet (Cooke, 1945), 25-35 feet (MacNeil, 1949), or 25-30 feet (Vernon, 1951 and Alt and Brooks, 1965) during the Yarmouth interglacial stage (Alt and Brooks, 1965). The 25-30 foot shore line possibly has been repeatedly occupied and may represent the predominant interglacial stand of sea level (Alt and Brooks, 1965). During this time the shape of Florida was much as it is today except that the peninsula terminated near Lake Okeechobee. There was a large oval island off the southwestern end of the peninsula. This region includes the Big Cypress Swamp, the Everglades, and the Florida Keys. The basin now occupied by Lake Okeechobee appears to have originated as a slight depression in the bottom of the Pamlico Sea. A long, wide lagoon was present through what is now the St. Johns River and extended southward from Orange Bluff on the St. Marys River to south of Sanford where the lagoon lay farther east and was separated from the ocean by narrow barrier islands (Cooke, 1939).

The Silver Bluff is the most recent of all terraces. This shore line was formed when the sea levels dropped to 5 feet (Cooke, 1939)

or 8 to 10 feet (MacNeil, 1949) above the present level. Previously thought to be Post-Wisconsin, it is now dated at the Sangamon interclacial by Alt and Brooks (1965). The intercoastal areas were narrowed in Silver Bluff time. The present sea level is probably merely a retreat from the Silver Bluff level (MacNeil, 1949).

The major surface streams of peninsular Florida flow parallel with the coasts throughout most of their length. They seem to have originated as narrow lagoons, bays, or sounds behind offshore bars of previous shore lines during periods of higher sea levels and probably resembled the present-day Indian River and similar lagoons which parallel the east coast of Florida (White, 1958). Since these rivers formed as a result of the build-up of bars off the coast lines of previous terraces, the rivers present on higher terraces are more ancient than those on lower terraces. Thus the Oklawaha River, which lies principally on the Penholoway and Talbot terraces, is older than the St. Johns River (Cooke, 1939). The major north-flowing streams, the St. Johns, Oklawaha, and Withlacoochee Rivers, all flow along troughs surrounded by higher terraces (White, 1958).

The geological history of the St. Johns and Oklawaha River systems is pertinent to an understanding of the distribution of populations of hubbsi and variegatus. The Oklawaha, St. Johns, and Mantanzas-Halifax-Indian River systems diminish in size, salinity, and percentage of marine fauna from east to west (McLane, 1955). If the theory of their geological origin is correct, the Oklawaha is the oldest system and the Mantanzas-Halifax-Indian River system the youngest. It would be expected that fewer marine relicts would remain in the

oldest basin, since these species would have been separated from the normal marine fauna a longer period of time (McLane, 1955). Thus Cyprinodon populations in the Oklawaha system have been isolated a substantial period of time. However, the ability of this species to penetrate great distances into fresh water rivers makes it difficult to date this isolation (Martin, 1972) and Cyprinodon in the Oklawaha system may not have to have been isolated since the time the basin was formed. C. v. hubbsi is the only fish that has shown any differentiation, although relict populations of Strongylura marina and Menidia beryllina are present (McLane, 1955). Since there is a poorly developed drainage connecting Lake Eustis with the Atlantic, it seems improbable that migration has taken place through the system (Carr, 1936b). Of the nine species of secondary-division freshwater fishes present in Florida, nine are Cyprinodontids and all have comparatively broad salinity tolerance. "If any species can trace its history from the Wicomico Islands, it is most likely one of this group," (Briggs, 1958:245).

The headwaters of the Oklawaha River are considered to be ancient depressions in the bottom of the Penholoway sea located south of a large estuary which existed in the present-day Oklawaha River Valley. Its principal source is in the group of large solution-basin lakes including Lake Griffin, Lake Eustis, Lake Apopka, Lake Yale, Lake Harris, and Lake Dora. These lakes are interconnected or are separated only by areas of peaty muck. The headwaters extend south through Lake Louisa and Lowery Lake and include several smaller lakes between. Some of these lakes in the upper reaches have probably been in existence

since Sunderland terrace (Upper Miocene) emerged from the sea, although most of the lakes in the headwater are of Penholoway origin (Cooke, 1939).

The Oklawaha rises in a zone of relict beach ridges which is one of the most prominent of the peninsula and generally follows a course parallel with the length of these ridges from its headwaters to its confluence with Orange Creek (a distance of some 75 miles). Although the river originally followed a trough between adjacent ridges, it seems that the course has been extensively altered by solution. This has caused it to thread through a long chain of lakes. The Oklawaha is also immediately west of a projected line which connects the Trail Ridge with the Lake Wales Ridge. "Thus it would seem to have been localized as a consequent stream, draining a lagoon between adjacent beach ridges of this group" (White, 1958:13). The pattern of drainage at the headwaters has been determined by the lakes rather than the lakes being remnants of a formerly continuous estuary (White, 1972). Thus it seems apparent that the headwaters arose independent of the Oklawaha River.

During the Aftonian interglacial period, when the sea was at the 42-foot level, the Withlacoochee River was a broad bay or estuary separated from the Gulf by narrow straits at Dunnellon (Johnson, 1972). The Withlacoochee has only lately acquired its course through the Brooksville Ridge at Dunnellon. The river previously arose as a lagoon on the Okefenokee terrace and followed a course parallel to the coast as does the Hillsborough River. At this time the Withlacoochee was a tributary of the Hillsborough. When the headwaters penetrated the Brooksville Ridge, the flow reversed. The Hillsborough

is now a tributary of the Withlacoochee River (White, 1958). In the past the headwaters of the Hillsborough and Oklawaha Rivers may have been captured by the Withlacoochee River. If this is true, it must have occurred before the bivalve Lampsilis teres reached the system since it exists only in the present Withlacoochee River (Johnson, 1972). "Perhaps the most plausible assumption concerning the earlier route of the Withlacoochee's escape from behind the ridge is that it went through the gap now occupied by the Hillsborough River east of Zephyrhills in Pasco County" (White, 1953:20). The central valley containing the Oklawaha and the western valley of the Withlacoochee are separated by the Sumter and Lake Uplands. A connecting valley, called the Lake Harris Cross Valley, for Lake Harris at its eastern end, exists between these uplands (White, 1972). If in the past the Withlacoochee did capture the headwaters of the Oklawaha River, it would have been through the Lake Harris Cross Valley, flowing along the course of the present-day Hillsborough River. Thus the last direct connection of the headwaters of the Oklawaha River may have been with the west coast of Florida rather than the east coast.

The St. Johns River is the dominant river of the east coast. From its headwaters in the meadows around Lake Helen Blazes (only 16 feet above sea level), the St. Johns River flows northward for nearly 200 miles. It is a young river since its upper valley (above Lake Harney) did not come into existence until Late Pleistocene time when a barrier island, now the east bank of the river, accumulated in the Pamlico Sea. Cooke (1939) assumed that the St. Johns River formed from a broad Pamlico lagoon that was enclosed by a coastal

ridge. However, White (1972) stated that the presence of these beach ridges may indicate that there was no lagoon but rather a regressional beach ridge plain and that the gradual breakdown of relict beach ridges with distance northward suggests that the route of the river was determined by and follows a course between relict beach ridges. The valley south of Lake Harney was composed of lagoons and sounds during Pamlico time, but these depressions were of earlier origin. The river depressions south of Palatka were formed by solution processes, while those north of Palatka were formed by stream erosion during pre-Pamlico and post-Talbot emergence (Cooke, 1939).

The evidence for the existence of a connection between the St. Johns with the sea south of Lake Harney consists of a convexity of the Pamlico terrace as it appears in the western valley wall of the St. Johns River opposite the Cape Canaveral area. In this area the terrace extends 10 to 20 miles farther east than it does at localities 30 to 40 miles up or down the coast (White, 1958). During the Pamlico time, nearly all of Brevard County probably was within this terrace. The chain of long, narrow barrier islands about three miles inland from the Indian River of today shut off a wide lagoon now followed by the St. Johns River. Whether the water in this lagoon was fresh or brackish is unknown (Cooke, 1945). The variegatus now present in the southern St. Johns River were probably derived from the east Florida coast through this connection, rather than from the mouth of the St. Johns River.

South Florida. In Pamlico time, when the sea was about 25 to 30 feet above its present level, most of the southern portion of the

Florida peninsula was a shallow submerged marine bank similar to the present-day Bahama Banks. At this time the southern shore of Florida passed north of Lake Okeechobee, although there are no relict shore lines in this distal zone of the peninsula (White, 1972).

Most of Indian River County was submerged in the Pamlico seas, but there were barrier islands not far inland to the present sea shore. Nearly all of both Broward and Palm Beach Counties were also covered by the sea. All of Dade and Monroe Counties were submerged while all but the west-central part of Lee and the northern part of Collier were under the sea (Cooke, 1945).

North of Palm Beach, the present-day coastline lies increasingly farther back from the edge of the continental slope. At Palm Beach the edge of the continental slope intersects the coast. In this area deep water is close to shore. The reason for this is not clear, but it probably results from the presence of the Florida current directly off shore in this area and from the rapid deposition of carbonates from the tropical water (White, 1972). The absence of variegatus and of killifishes in general from this area has already been noted (Christensen, 1965; and Relyea, personal communications) and it is interesting to speculate that this distributional hiatus is somehow related to these geological features.

Florida Keys. The Florida Keys are of two types, the upper Keys (Key Largo to Bahia Honda Key inclusive) and the lower Keys (from Bahia Honda to Key West). The upper Keys are of coral reef formation, now called Key Largo limestone, and may be further divided into the high and low coral Keys with the boundary occurring between Upper and

Lower Matecumbe Keys. The lower Keys have been formed from Miami oolite, the same formation making up the eastern rim of the peninsula in the Everglades. This shoal extended, with a few breaks, westward to the Dry Tortugas. The continuation beyond Key West is now marked by the Marquesas Keys and a few smaller islands (Cooke, 1939, Duellman and Schwartz, 1958, and White, 1972).

The coral Keys evidently were formed as coral reefs that grew at the edge of deep water in the Pamlico sea. The high coral Keys seem to have been an active coral reef at the time the Miami Ridge of the lower Keys was emerging to form mangrove islands. The surface of the low coral Keys closely resembles that of lower parts of the high coral Keys and gives every indication of having been formed in the same way but at a sea level some four or five feet higher than the present sea level. They were subsequently worn down by solution along the shore line of the sea. The older high coral Keys were cut at some earlier Pleistocene time when the sea level was about ten feet higher than present (White, 1972).

The oolite Keys extend northeastward behind the southwestern end of the coral Keys and become sparse in distribution until they disappear beyond East Bahia Honda Key. There is little doubt that the Miami Ridge and the oolite Keys formed in the same way at opposite ends of the coral reef that now makes up the coral Keys. Both formed during Pamlico time, probably at a sea level ten feet higher than the present level. White (1972:21) stated that "all the coral rock of the Key Largo formation should be Pamlico age or older. And since the oolite of the oolite Keys has the same age, it too should have been made during the Pamlico high level of sea."

Before the coral reef Keys emerged from the sea, a land connection existed across Florida Bay from the mainland in the Everglades to the lower Keys. When the area that is now Florida Bay submerged, the lower Keys were isolated. Later when sea level was four feet higher than the present level, the coral reef emerged to form the upper Keys, and thus the present chain of islands was formed from the mainland. Duellman and Schwartz (1958) detail biological and geological evidence to support the theory that a connection between the lower Keys and the southwestern mainland did not involve the upper Keys.

Environmental Considerations

Much has been written in the past on environmental factors influencing the distribution of Cyprinodon (Cowles, 1934; Miller, 1950; Gunter, 1956, 1967; Simpson and Gunter, 1956; Barlow, 1958a,b; Renfro, 1960; Martin, 1967, 1968; Strawn and Dunn, 1967; Brown and Feldmeth, 1971; Hill and Holland, 1971; Renfro and Hill, 1971; Echelle et al., 1972; Renfro and Hill, 1972; Naiman et al., 1973; Otto and Gerking, 1973).

Cyprinodon variegatus is extremely tolerant of changes in temperature and salinity and is believed by Gunter (1967:238) to be "the toughest aquatic animal in North America." Possibly the most resistant of all fishes to variations in the chemical and physical environment, C. variegatus will usually be the predominant cyprinodontid in areas where virtually all other fish life is absent.

C. variegatus can tolerate a very wide range of salinity, especially towards the higher ranges. Simpson and Gunter (1956:124)

collected C. variegatus from areas where the salinity was as high as 142-147 ppt, but emphasized that "water at such salinity is not sea water for some salts are precipitated before sea water attains such concentration and the salt complex is changed." Eggs of variegatus can hatch in water where salinities are in excess of 110 parts per thousand (ppt) (Renfro, 1960). Martin (1972) described breeding populations of Cyprinodon in a range of 0.08-97.3 ppt salinity, spawning from 0.08-63.1 ppt and newly hatched young in excess of 90 ppt. Gunter (1945) collected specimens from waters with a salinity of 71.5 ppt; seventy-nine days later, following a period of rain, variegatus was still present at a salinity of 2.2 ppt.

The preferred salinity range of C. variegatus is as variable as its salinity tolerance. Simpson and Gunter (1956) found variegatus most abundant as 20-36.9 ppt. Station salinities weighted by the number of fish caught, showed a mean salinity of 2.8 ppt in the Caloosahatchee estuary (Gunter and Hall, 1965). Kilby (1955) collected variegatus at Bayport and Cedar Key over a range of 0.0-35.6 ppt. Preference was shown for salinities less than 20 ppt. The species was most often caught at salinities of 10-25 ppt by Gunter (1945) and was less common above that range than below.

Other Cyprinodon species are also noted for their euryhaline ability. In the western areas of the United States Cyprinodon has been found to be exceedingly common, probably because of its tolerance of extreme variations in water temperature and salinity (Cowles, 1934). Barlow (1958b) found that the maximum salinity tolerance of young C. macularius, in the field, was approximately 90 ppt; however, adults were somewhat less tolerant.

The Red River Pupfish, C. rubrofluviatilis, can detect and positively select saline concentrations comparable to those for which they had been acclimated. Hill and Holland (1971) state that the selection ability is due to quantitative sensitivity and is of significant survival value since the saline concentrations of the streams they inhabit fluctuate drastically. The ability of C. rubrofluviatilis to adapt to rapid changes as well as extremely high salinities has been shown to be a result of the formation of apical crypt areas in Key-Willmer gill cells. These cytological changes serve to increase the amount of gill surface area in contact with the external medium, and seem to be identical to those of C. variegatus (Renfro and Hill, 1972). A study by Renfro and Hill (1971:714) has shown that "salinity has probably posed no serious selective hazard to the pupfish. Regulatory ability has apparently placed no restriction on this fish with respect to habitat." Although intraspecific variation in the osmotic ability of C. variegatus from the Texas coast has been noted by Martin (1968), this was due largely to environmental factors, such as the salinity during development, rather than genetic factors.

Cyprinodon variegatus is also eurythermal. Miller (1948) stated that Cyprinodon can tolerate virtually the hottest known natural waters. The salt marsh cyprinodonts are, as a group, the most resistant fishes to heat death at various salinities and C. variegatus appears to be the most resistant of the species yet tested. Cyprinodon variegatus acclimated to fresh water and 35°C and tested at one-half degree intervals from 40.5° to 43.0°C showed mean survival times of 808, 173, 116, 56.4, 28.5, and 18.5 minutes (Strawn and Dunn, 1967). Addition

of some dissolved solids to fresh water increased survival time at higher temperatures (Strawn and Dunn, 1967; and Otto and Gerking, 1973). Otto and Gerking (1973) reported that in all these respects C. variegatus was slightly more heat tolerant than the desert pupfish, C. milleri. Warlen (1964) reported a temperature range of 2-33°C for C. variegatus. Harrington and Harrington (1961), however, reported young variegatus in a shallow pond in which the temperature had risen to 43°C. Warlen (1964:26) found only small variegatus in pools with temperatures above 29°C and stated that "this might indicate that small variegatus possess a higher incipient lethal temperature than larger ones." Naiman (1973) reported an upper lethal limit of temperature tolerance of 38°C and a critical thermal maximum of 43°C for C. milleri, but noted that these temperatures are never reached in the deeper waters in which the species is found. He concluded that midsummer water temperatures had no severe selection pressure for heat tolerance in this pupfish. Naiman (1973) did, however, suggest selection for tolerance of wide temperature ranges. Some pools inhabited by milleri have daily temperature fluctuations of 14.8°C.

Cyprinodon macularius and C. rubrofluviatilis eggs have been hatched at the highest incubation temperatures reported in the literature, 35.8°C and 36.4°C, respectively, (Kinne and Kinne, 1962; and Echelle et al., 1972). The upper lethal limit for the adults of C. rubrofluviatilis slightly exceeds these values (Echelle et al., 1972). Barlow (1958a) noted that C. macularius tended to avoid temperatures above 36-37°C by moving between shallow and deep areas in response to daily fluctuations in temperature. Cyprinodon diabolis is isolated

in a thermally constant desert spring in which the present temperature of 33.9°C is only nine or ten degrees below the lethal temperature. Surprisingly, these fish and other species of Cyprinodon which exist in thermally constant springs have the same abilities to withstand extreme temperatures and to acclimate as do Cyprinodon which inhabit streams and marshes where temperatures fluctuate as much as 20° daily and more than 40° seasonally (Brown and Feldmeth, 1971).

Cyprinodon variegatus is also resistant to cold and has never been found along open shores of the Texas coast following fish-killing freezes (Simpson and Gunter, 1956). Rinckey and Saloman (1964:9) collected variegatus unharmed in Tampa Bay during hard freezes when "The bottom was completely covered with (dead) fish." During these freezes, and the cold parts of the year, variegatus are found away from shore in deeper water (Springer and Woodburn, 1960). Gunter (1945) also suggested that C. variegatus moves to deeper water in response to lower temperatures.

Factors Influencing Local Distribution in Florida

As already noted, the Pamlico terrace was formed when the sea rose to a level of 25-30 feet above the present level during the Yarmouth interglacial stage (Alt and Brooks, 1965). Areas submerged below the Pamlico Sea correspond almost exactly with present-day ground water salinities greater than 100 ppm and surface water chlorinities of 25-1000 ppm (salinities of 75-1835 ppm)(Odum, 1953). The distribution of Cyprinodon populations in the fresh waters of Florida, except for hubbsi, also corresponds to the area occupied by the Pamlico terrace (Figure 1).

The high chlorinity in the fresh waters of Florida is due primarily to salt deposits held in the sediments from times when these areas were submerged. The lack of extensive salt inside the area occupied by the Pamlico terrace suggests that enough time has elapsed since submergence for the salts to have been flushed out of the sediments. The water which is being flushed out of the sediments of Florida has ions in ratios different from those of sea water, some ions in lower concentrations due to dilution and others higher due to solution (Odum, 1953).

Chlorinity data from Odum (1953) for fresh water areas known to be inhabited by Cyprinodon are: 150-200 ppm (salinity 300 to 390 ppm) between Lake Winder and Lake Harney in the St. Johns River, 227 ppm (salinity 440 ppm) in Lake Monroe in the St. Johns River, 35-100 ppm (salinity 93-210 ppm) in canals leading out of Lake Okeechobee. Proceeding north from the town of Everglades, chlorinity in Rt. 29 canal is 945 ppm (salinity 1736 ppm) at Rt. 41 junction, 116 ppm (salinity 240 ppm) four miles north of this junction, and 16-60 ppm (salinity 59-138 ppm) in Lake Okeechobee. The chlorinity of the lakes from which C. hubbsi is found at the headwaters of the Oklawaha River vary from 12.8 ppm (salinity 53 ppm) in Lake Harris to 26.8 ppm (salinity 78 ppm) in Lake Weir (Brezonik et al., 1969). McLane (1955) reported salinities as high as 10 ppt in the Salt Lake region of the St. Johns River during periods of low water. Cyprinodon is abundant in these waters. Bensen (Green) Springs at Lake Monroe has a salinity of 7.0 to 3.4 ppt (McLane, 1955). (Salinity is equal to the chlorinity, stated in grams per kilogram, multiplied by 1.805 and adding 0.03; it is expressed in parts per thousand [Coker, 1962]).

Many other organisms have been characterized as having distributions which penetrate fresh waters of Florida to those areas occupied by the Pamlico seas or chlorinities as low as 25 ppm. In addition to C. variegatus, other fishes are snook (Centropomus sp.), tarpon (Megalops atlanticus), sheepshead (Archosargus probatocephalus), mangrove snapper (Lutjanus griseus), channel bass (Sciaenops ocellata), and blue crab (Calinectes sapidus) (Odum, 1953). The killifish Fundulus confluentus also seems to have a Pamlico terrace distribution (Relyea, personal communications).

Some species of hydrobiid snails are also restricted to the ocean side of the Pamlico terrace. Since the terrace was formed during the Yarmouth interglacial, Johnson (1973) stated that the distribution of these suggests that they came from elsewhere, or speciated rapidly. Included in this group are two species of Littoridinops, Heleobops docima, two species of Onobops, Pyrgophorus platyrachis, and various species of Aphaostracon (Thompson, 1968; and Johnson, 1973). The distribution of the genus Aphaostracon in the fresh waters of Florida (Thompson, 1968) corresponds almost exactly to the distribution of Cyprinodon.

The geological history and resulting high salinities of the St. Johns River south of Lake Harney explain the presence of five marine Crustacea, two marine polychaete worms, and nine species of marina fishes. Most of these forms are permanent breeding populations rather than migrants entering from the sea (McLane, 1955). Further evidence for the late formation of the St. Johns River below Lake Harney is the presence of saline water in the principal artesian aquifer of the

area. During the Pleistocene, sea water infiltrated the artesian aquifer. After the high seas declined, fresh water entering the aquifer began diluting and flushing out the salt water. In most areas this flushing is complete, but in areas south of Lake Harney, distant from recharge areas, the flushing is still incomplete (Wyrick, 1960).

Many species of fish and Crustacea, such as the blue crab, penetrate from the Atlantic into the freshwaters of the upper reaches of the St. Johns River (Tagatz, 1967). The main reason for this movement is the abundance of calcium chloride in the water, much of which comes from the many salt springs that drain into the river (Odum, 1953).

No fish are present in the St. Johns drainage which are specifically distinct from its typical marine relative. There are, however, disjunct, isolated breeding populations that have undergone some degree of differentiation. Six species of fish, including Cyprinodon variegatus, are present in this group (McLane, 1955). Three brackish water bivalves are found far upstream in the St. Johns and endemic species of Hydrobiidae are found in many springs of the river (Johnson, 1972).

Gunter (1956) agreed with Odum (1953) that sensitivity to chloride is the most important factor determining the distribution of estuarine animals. Gunter (1956:618) stated that "animals distribute themselves over definite salinity ranges and seem to be quite sensitive to salinity differences near the lower side of these ranges." McLane (1955) found that C. variegatus reached its upstream limit in the St. Johns River where the salinity decreased from 10.7 ppt to .028 ppt.

Breder (1934) indicated that the presence of marine fishes, including Cyprinodon baconi (= variegatus according to Miller, 1962)

in Lake Forsyth, Andros Island, was due to the presence of a sufficient amount of calcium in the water. However, Martin (1972) indicated that calcium plays a minor role, if any, in the distribution of Cyprinodon. He stated that "Cyprinodon variegatus is probably not limited in its distribution by levels of Ca, Mg, Na, or K, nor by ratios of these ions in most situations" (Martin, 1972:93) and demonstrated that the majority of stations where Cyprinodon did not occur had levels of these ions within the range at which the species was found. He concluded that the distribution of Cyprinodon was restricted by a biological rather than a physio-chemical factor. The presence of primary freshwater fish was thought to be the most important factor limiting entrance into freshwaters. No overlap in distribution with centrarchids and little with cyprinids was noted. Echelle et al., (1972) also concluded that interspecific interactions were the primary factors limiting the distribution of C. rubrofluviatilis.

However, Beckman and Mettee (1974) disputed the conclusions of Martin (1972) and provided additional data concerning the species associations of Cyprinodon. They believed that inadequate sampling by Martin resulted in erroneous conclusions regarding species associations and local distribution of C. variegatus. The results of Martin (1972) are also contradicted by Christensen (1965), who found that Lepomis macrochirus and Micropterus salmoides were among the principal associates of Cyprinodon collected from freshwaters of the West Palm Beach area. I have also noted that the centrarchids are among the most abundant fishes caught with variegatus in Salt Lake of the St. Johns River.

Harrington and Harrington (1961) have suggested competitive feeding relationships between C. variegatus and other Cyprinodonts. The diets of Cyprinodon and Poecilia latipinna were reported to be indistinguishable when analyzed volumetrically. I see no evidence, however, that this supposed interaction influences the distribution of either species. Commenting on the distributional hiatus of estuarine cyprinodontids in the Jupiter area of West Palm Beach County, Christensen (1965:267) stated that "the restriction of some cyprinodonts to fresh water and the absence of others is probably due to the lack of suitable habitat and the abundance of gerrids especially Eucinostomus argenteus, throughout the area." Although Christensen (1965) noted that his evidence was largely circumstantial, there is no overlap in the ranges of the gerrids and the cyprinodontids. At Cedar Key, Kilby (1955) noted that there was a negative correlation between the occurrence of E. argenteus and C. variegatus and Fundulus confluentus. On the northern Gulf coast gerrids are lacking and cyprinotontids are abundant. In south Florida the gerrids penetrate much farther into fresh waters than they do in the north (Christensen, 1965). Martin (1972) noted no exclusion of Cyprinodon by marine species.

Christensen's theory would be easier to accept were it not well established that cyprinodontids are usually ecological dominants in their environment (Gunter, 1945, 1950; Kilby, 1955; Simpson and Gunter, 1956). Kilby (1955), for example, found that over 40,000 out of 54,687 or 74% of the fish caught in two Gulf coastal marshes were cyprinodontids.

Despite euryhaline and eurythermal abilities and the apparent lack of other intrinsic limiting factors, Cyprinodon variegatus is

essentially restricted to the more saline waters in its "fresh water" range on the Pamlico terrace. Renfro and Hill (1971) have shown that salinity variation is of no serious selective disadvantage to Cyprinodon species. No habitat restrictions are placed on the species as a result of regulatory ability. Kinne and Kinne (1962) have noted, however, that C. macularius is metabolically more efficient at salinities of 15-35 ppt than in fresh water and was most efficient at 15 ppt. Echelle (1970) found that the rather limited geographical range of C. rubrofluviatilis was due to its adaption to a broad ecological niche resulting in a great deal of competition with other species at low salinities. This competition is greatly reduced at higher salinities because only a few species occupy the typical saline habitat of the pupfish. In extreme environmental situations, C. variegatus seems less able to compete, and a salinity of about 13 ppt favors a healthy population (Kaill, 1967).

Habitat, food availability and other biological factors are probably of little importance in limiting the distribution of Cyprinodon in Florida. McLane (1955) has noted that extensive suitable shore-line habitats exist in the St. Johns River but variegatus is restricted to the southern sections of the river. The shores and bottom of Lake Jessup in some areas seem identical to those of Lake Harney in the St. Johns but variegatus seems absent from Jessup and abundant in the nearby, more saline Lake Harney. The food preferences of Cyprinodon have been shown to be quite broad and variable (Harrington and Harrington, 1961; and Martin, 1970). These preferences are "so broad as to not have great effect on local distribution" (Martin, 1972:89).

Although no one chemical or biological factor may limit its distribution, there is no doubt that variegatus is restricted to more saline waters of the Pamlico terrace and coastal areas. The distribution of Cyprinodon populations also appears to reflect not only current environmental conditions, but also past geologic events. Thus it seems that variegatus distribution may be limited by a combination of factors including a physiological stress on the pupfish as they invade fresh waters. A physiological stress may result from a number of direct and indirect limiting factors, including a less efficient metabolism making variegatus less able to compete.

RESULTS AND DISCUSSION

Counts

Dorsal Rays (Table 1). Dorsal fin rays are of little value in distinguishing any morphological variation among Florida Cyprinodon populations. Most populations have modally 11 dorsal rays. Within Florida no geographic trends exist among populations and the count does not appear to be affected by either salinity or temperature. LaBounty (1972) found increased dorsal ray counts with decreased salinity in desert Cyprinodon.

Miller (1962) found that C. baconi (= variegatus) from the Bahamas had 9 to 11, usually 10, dorsal rays. Jordan and Evermann (1896) reported that variegatus had 11 dorsal rays while riverendi had 10. Other investigators have reported that C. hubbsi usually has 11 dorsal rays (Carr, 1936a), C. v. artifrons usually 10 (Hubbs, 1936) and C. variegatus usually 10 (Chipman, 1958). The literature suggests that individuals with 10 dorsal rays predominate in Mexico and along the northern shores of the Gulf of Mexico (Baird and Girard, 1853; Jordan and Gilbert, 1882; Hubbs, 1936; Chipman, 1958).

Anal Rays (Table 2). No geographic clines or effects on mean values by variations in salinity or temperature among populations are noted. The number of anal rays is of no diagnostic value in Florida Cyprinodon. Carr (1936a,b) indicated that hubbsi was unique in

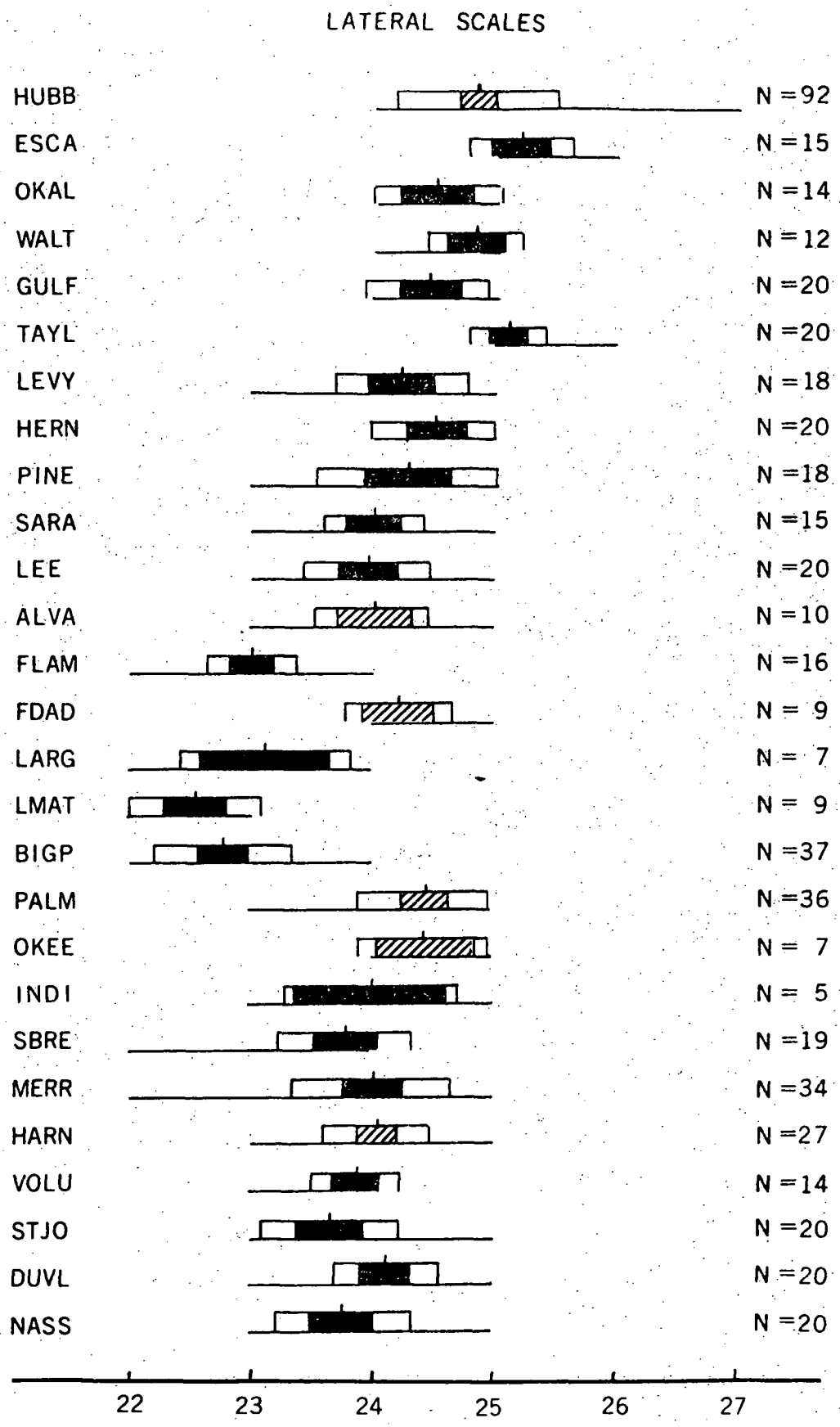
possessing 11 anal rays but my data show that hubbsi cannot be distinguished from other Florida Cyprinodon populations on this basis. Hubbs (1936), Miller (1962) and Chipman (1958) have reported that C. variegatus usually has 10 anal rays. Jordan and Evermann (1896) stated that riverendi has 9 anal rays. No south Florida Cyprinodon populations show any mean values this low. LaBounty (1972) noted a decrease and Chipman (1958) an increase in the number of anal rays with increased salinity.

Caudal Rays (Table 3). The number of caudal fin rays tends to be slightly lower in populations from south Florida than from adjacent areas on both the east and west coast. A slightly lower average is indicated in the area from Lee County through the Keys to Lake Okeechobee. Within the subspecies of C. variegatus, Hubbs (1936) reported that artifrons had 14, variegatus 15-17, and ovinus 14-15 caudal rays. Florida populations cover this entire range. Freshwater populations show no significant variation in the number of caudal rays from adjacent coastal areas.

Lateral Scales (Figure 2, Table 4). Hubbs (1936) reported that C. v. riverendi from Cuba had 22-23 lateral scales; however, no values were given for Cyprinodon (possibly riverendi) from the Keys. Although methods of counting were probably different, both Breder (1932) and Jordan and Evermann (1896) reported that variegatus had 26 and riverendi 24 lateral scales. The results shown in Figure 2 demonstrate the existence of coastal populations in south Florida and the Keys which have fewer lateral scales (22-23) than those from adjacent areas. Further investigation of Caribbean Cyprinodon populations are

FIGURE 2

Lateral scale counts in Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


LATERAL SCALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE
SARA
LEE
ALVA
FLAM
FDAD
LARG
LMAT
BIGP
PALM
OKEE
INDI
SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N =92
N =15
N =14
N =12
N =20
N =20
N =18
N =20
N =18
N =15
N =20
N =10
N =16
N = 9
N = 7
N = 9
N =37
N =36
N = 7
N = 5
N =19
N =34
N =27
N =14
N =20
N =20
N =20
22
23
24
25
26
27

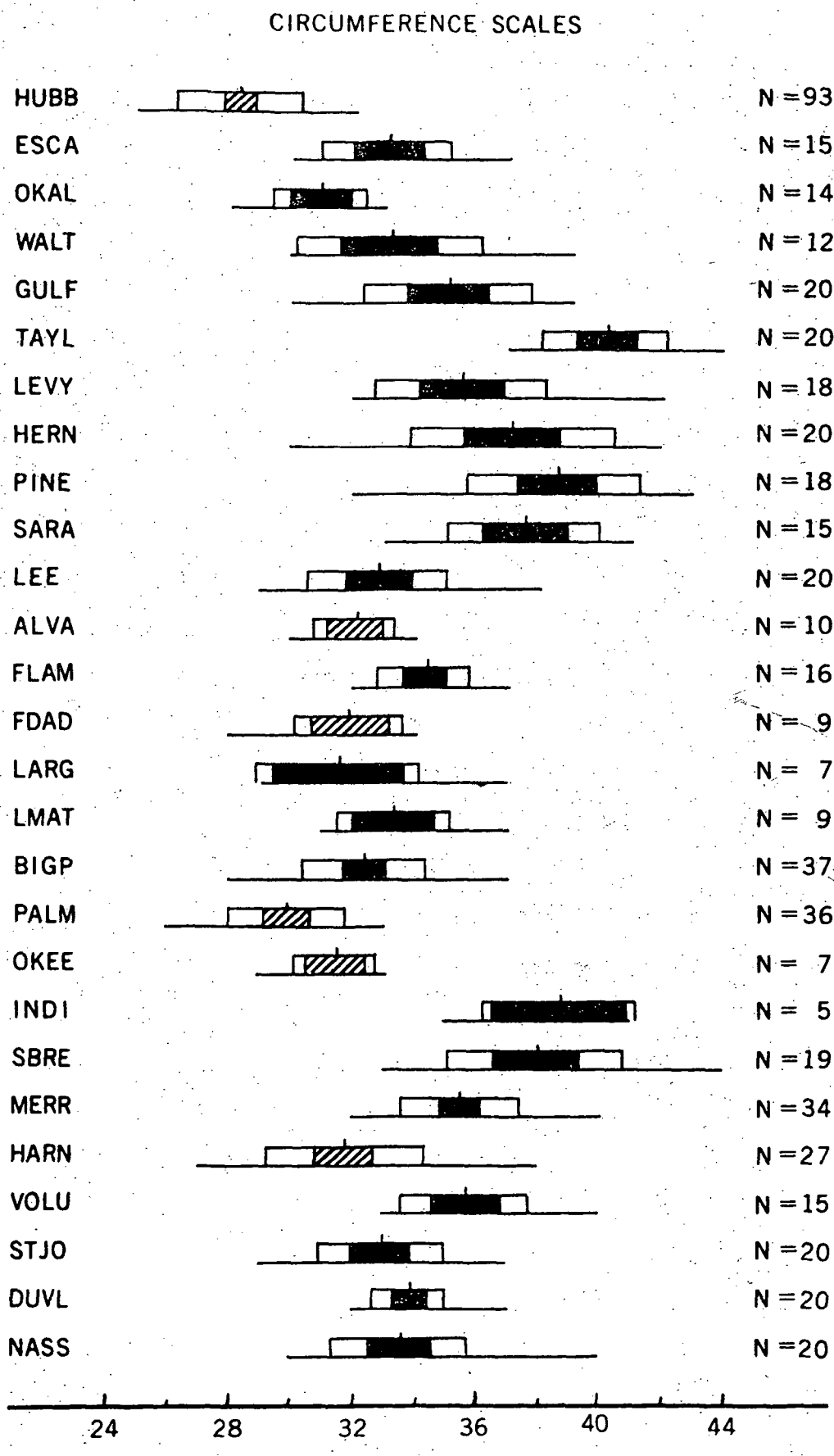
needed to determine the relations of south Florida Cyprinodon with Cuban riverendi. Miller (1962) stated that C. variegatus from the Bahamas have 24-25 lateral scales. Figure 2 also shows populations of hubbsi to have slightly more lateral scales than other Cyprinodon. Carr (1936a) stated that hubbsi usually had 25-26 scales. A clinal decrease in the number of scales is indicated from the northern west coast, south through the Florida Keys. No effect on the count by temperature or salinity is noted since freshwater populations show little variation in mean values from adjacent coastal populations. Both Chipman (1958) and LaBounty (1972) found that populations of Cyprinodon from more saline environments generally have higher lateral scale counts.

Predorsal Scales (Table 5). Little variation in the average number of predorsal scales was observed among populations of Florida Cyprinodon, although populations from Lee County to Big Pine Key generally have slightly lower means. Both Chipman (1958) and Gilmore and Williams (unpublished manuscript) reported little variation in the number of predorsal scales, with a range from 9 to 11. Freshwater populations show little change from coastal Cyprinodon although Chipman (1958), Miller (1950) and LaBounty (1972) noted increases in counts with increased salinity. No geographic pattern of average counts is evident in the populations studied.

Circumference Scales (Figure 3, Table 6). Average circumference scale counts among populations increase southward until Sarasota County on the west coast and Indian River County on the east is reached. More southerly populations abruptly fall out of this clinal pattern and have

FIGURE 3

Circumference scale counts in Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


CIRCUMFERENCE SCALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE
SARA
LEE
ALVA
FLAM
FDAD
LARG
LMAT
BIGP
PALM
OKEE
INDI
SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N =93
N =15
N =14
N =12
N =20
N =20
N =18
N =20
N =18
N =15
N =20
N =10
N =16
N = 9
N = 7
N = 9
N =37
N =36
N = 7
N = 5
N =19
N =34
N =27
N =15
N =20
N =20
N =20
24
28
32
36
40
44

much lower counts than adjacent populations to the north. The east and west coastal clines suggest that increased temperature may result in higher counts. This contradicts Miller (1948, 1950) and LaBounty (1972) who reported circumference scale counts of Cyprinodon increase with decreased temperature. There is also an indication that circumference scale counts are slightly lower in freshwater populations than adjacent coastal areas (Figure 3). In this regard the results of Miller (1948, 1950) and LaBounty (1972) are supported. Populations of hubbsi possess the lowest scale counts, but other freshwater populations also exhibit a shift toward decreased counts. Miller (1962) reported that C. baconi (= variegatus) had 26-32, usually 30, scales and Chipman (1958) stated that variegatus had 26-39, usually 31, circumference scales with no salinity relationship.

Dorsal Origin to Belly Midline Scales (Table 7). Dorsal origin to belly midline scale counts and all other vertical body scale counts reflect the same geographical pattern as is shown in Figure 3 for circumference scales. A definite increase in average scale counts south along both the east and west coast indicate a possible influence by temperature. In contrast to this cline, scale counts suddenly are reduced in populations in south Florida from Lee County and the Keys to Lake Okeechobee. A slight reduction in the number of scales in freshwater populations is also demonstrated. The population of hubbsi has the lowest values for this count; however, it is closely followed by other freshwater populations.

Dorsal Origin to Anal Origin (Table 8). These data exhibit the same geographical patterns as dorsal origin to belly midline scales.

A further discussion is included under circumference scales. Miller (1962) reported that C. variegatus from the Bahamas usually had 11-12 scales for this count. This would approximate the lowest counts for Florida Cyprinodon which are from fresh water. Miller (1948, 1950) and LaBounty (1972) noted that this count may increase with increased salinity in Cyprinodon.

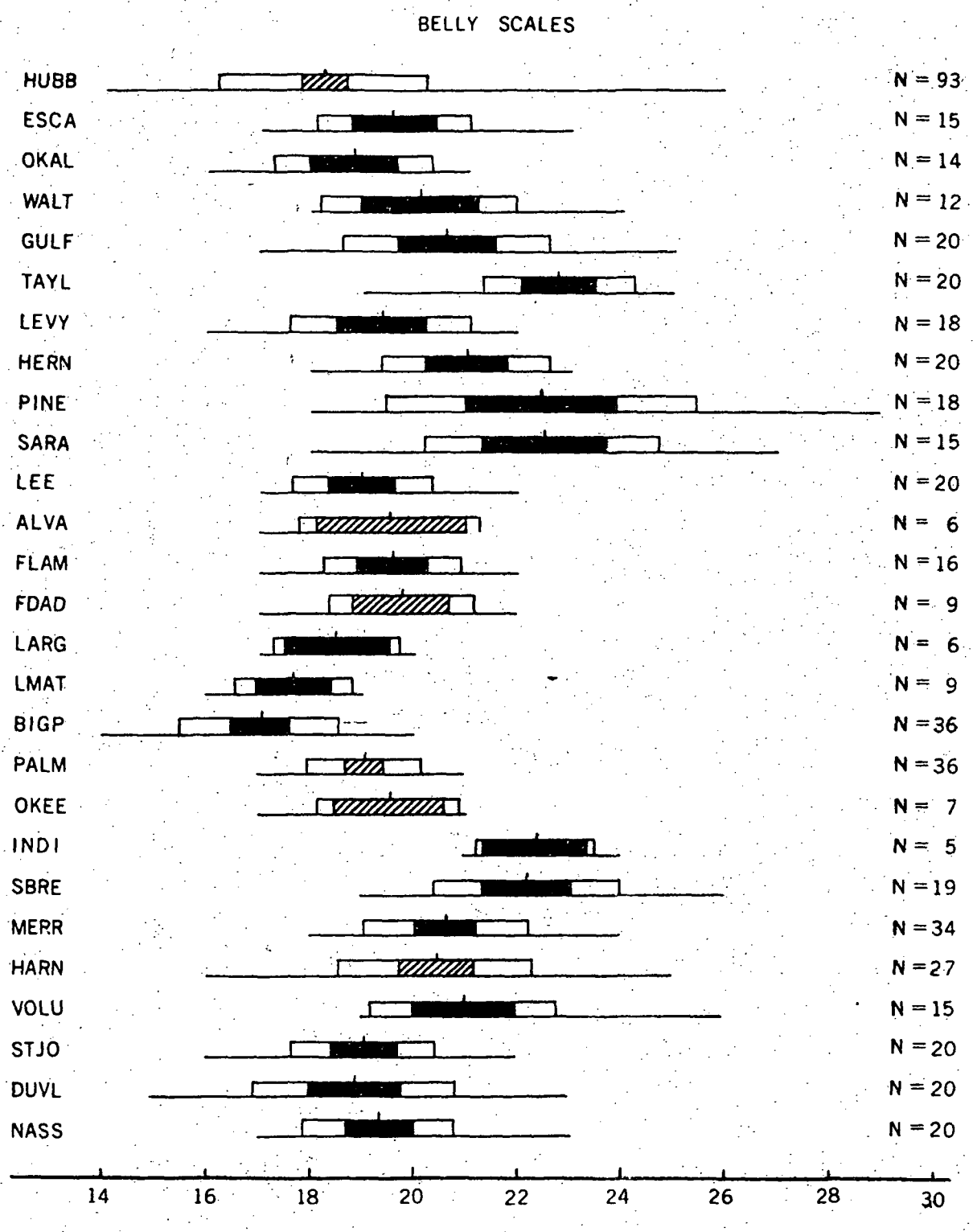
Dorsal Origin to Pelvic Origin (Table 9). These data follow the same variational patterns as the preceding two scale counts. Further discussions are included under circumference scales. Miller (1962) reported that Bahamian C. variegatus have from 11-13, usually 12, scales from the dorsal origin to pelvic origin. This count may also increase with increased salinity (Miller, 1948, 1950; LaBounty, 1972).

Belly Scales (Figure 4, Table 10). Belly scales show the same pattern of geographical variation as circumference scale counts, an increase in the number of scales as one proceeds southward. Little or no influence by variations in salinity is noted for this character since average values of freshwater populations deviate little from adjacent coastal populations. A possible temperature influence is noted--northern coastal populations having fewer belly scales than southern groups. The distinctiness of south Florida populations is clear. Carr (1936a) stated that more scale rows were present on the belly of west coast variegatus than those from the east coast but the data show that at comparable latitudes there is no noteworthy difference.

Suborbital Scales (Table 11). Only slight geographical variation is observed for this character. The west coast populations show no

FIGURE 4

Belly scale counts in Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


BELLY SCALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE
SARA
LEE
ALVA
FLAM
FDAD
LARG
LMAT
BIGP
PALM
OKEE
INDI
SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 93
N = 15
N = 14
N = 12
N = 20
N = 20
N = 18
N = 20
N = 18
N = 15
N = 20
N = 6
N = 16
N = 9
N = 6
N = 9
N = 36
N = 36
N = 7
N = 5
N = 19
N = 34
N = 27
N = 15
N = 20
N = 20
N = 20
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variation while mean values of east coast populations seem to decrease slightly proceeding northward. Low scale counts are present in those populations from Lower Matecumbe and Big Pine Keys. No environmental influence by temperature or salinity on this scale count is indicated.

Preorbital Scales. Moore (1968) and Miller (1962) state that C. variegatus is typically well scaled up to or beyond the level of the uppermost preorbital pore while hubbsi typically has no scales above the middle of the pupil (Moore, 1968). No Florida Cyprinodon are typically well scaled above the level of the fourth preorbital pore or the middle of the pupil. All populations are, however, scaled above the level of the nostrils.

Frontal Scales (Table 12). Cyprinodon populations from the northern east coast of Florida, especially near the mouth of the St. Johns River, have reduced scalation on top of the head. No other patterns of average counts are evident in this character. The population from Lake Harney in the St. Johns River possesses frontal scalation like Cyprinodon from nearby Merritt Island on the coast, not like populations from the mouth of the St. Johns at Duval County. Limited observations of variegatus from the northeast United States indicate that the northeast Florida trend does not continue northward up the east coast of the United States. However, Hoedeman (1958) reported only 3.5 frontal scales (adapting his data to the methods employed herein) for "typical" Cyprinodon. Only 1.5 scales were drawn in front of the large scale between the eyes (overlaps both scales in front and behind) whereas Florida Cyprinodon usually have 3.0 in this area.

Measurements

Standard Length (Table 13). Specimens of hubbsi appear to be smaller than other Cyprinodon; however, they attain a much larger size than reported by Carr (1936a). Carr reported that adult males range from 20-27 mm SL and adult females 23-31 mm SL. The largest specimen of hubbsi examined in this study was 41.2 mm SL or about 52 mm total length. Average lengths in mm reported for C. variegatus are as follows: Hildebrand (1917), 45 for females and 48 for males; Gunter (1945, 1950), 43; and Simpson and Gunter (1956), females 46 and males 45. The largest specimen of C. variegatus yet reported was 93 mm total length (Gunter, 1945). Warlen (1964) stated that C. variegatus hatch at a length of 4 mm, attain a length of 20 to 34 mm at the end of one year, and 38-45 mm at two years. Chipman (1958) reported a strong correlation between greater standard lengths and increased salinity. The present study cannot demonstrate a general relationship of this type.

Body Depth (Figures 5 and 6, Table 14). Body depth has been used by Carr (1936b) and Moore (1968) as a diagnostic character for the separation of hubbsi and variegatus. Both reported that the body depth of hubbsi was less than 33 percent of standard length while variegatus was greater than 33 percent. The data indicate that this character varies greatly and probably is influenced by both environmental factors (salinity) and random genetic variation. Although populations of hubbsi have the least body depth of any Florida Cyprinodon populations, other freshwater groups also show a reduction in depth compared with adjacent coastal areas. Thus it is apparent

FIGURE 5

Body depth expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

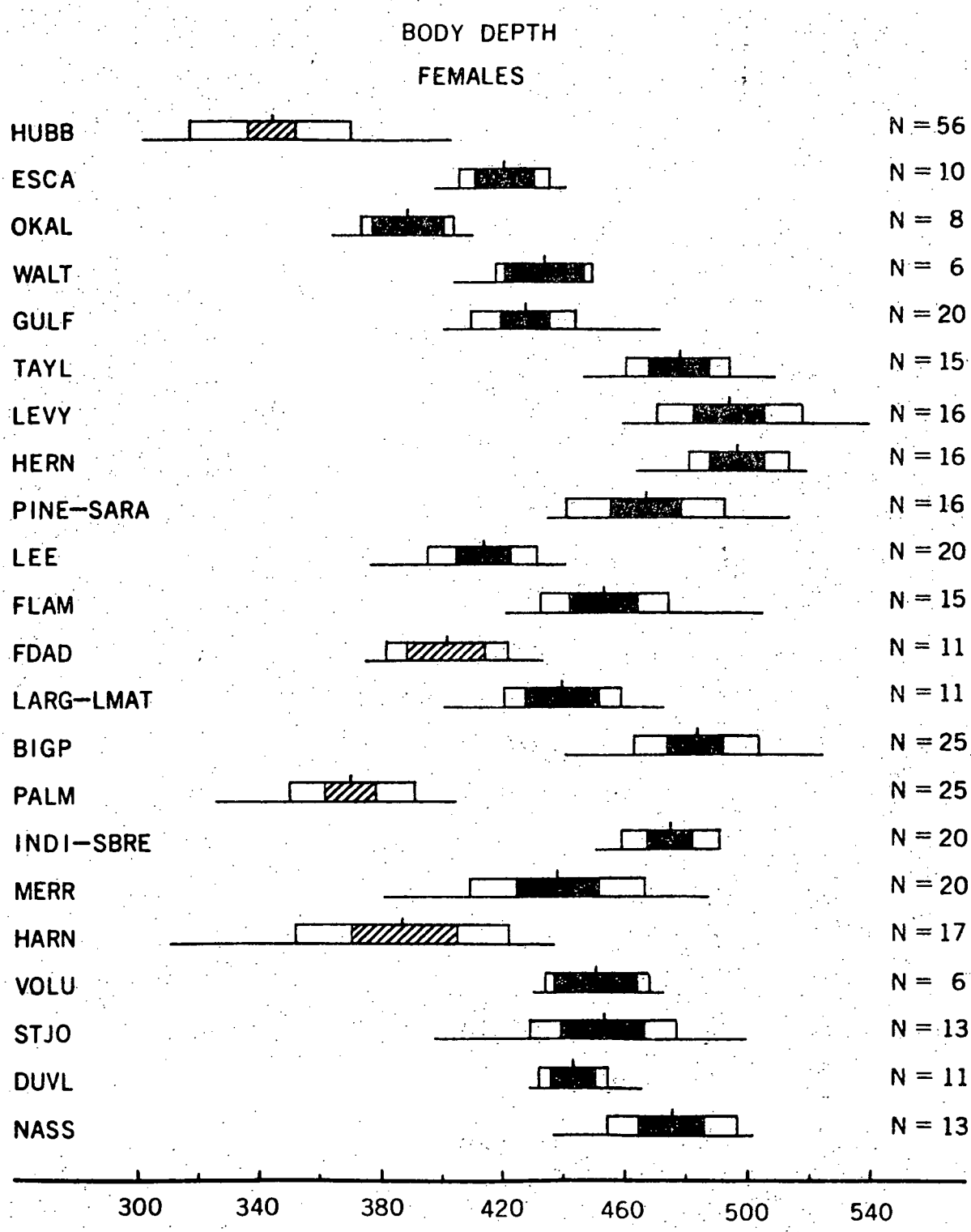
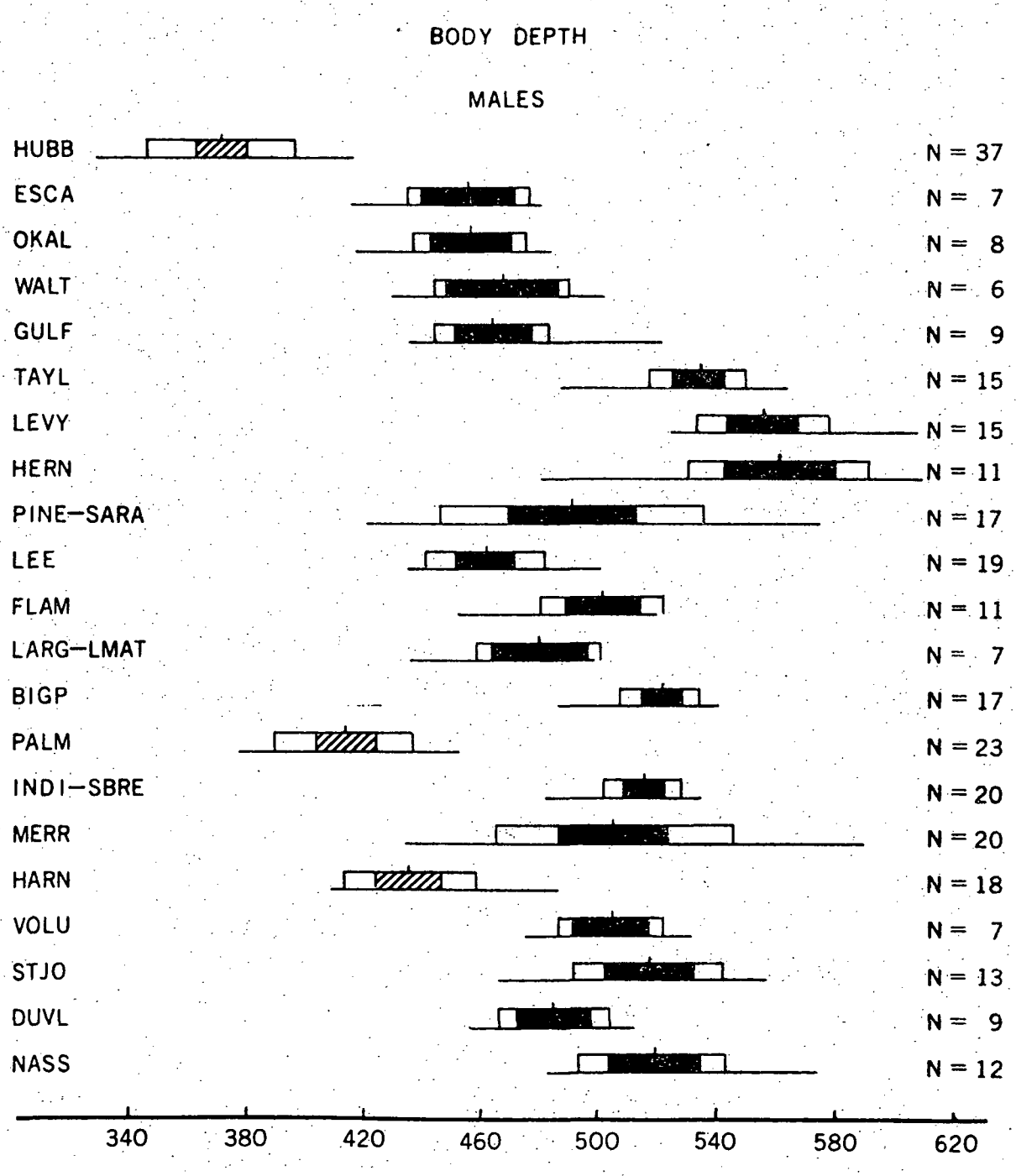

BODY DEPTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 16
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
300
340
380
420
460
500
540

FIGURE 6

Body depth expressed as thousandths of standard length for males of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


BODY DEPTH
MALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 37
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N = 8
N = 6
N = 9
N = 15
N = 15
N = 11
N = 17
N = 19
N = 11
N = 7
N = 17
N = 23
N = 20
N = 20
N = 18
N = 7
N = 13
N = 9
N = 12
340
380
420
460
500
540
580
620

that body depth is not of great value for diagnostic purposes. Breder (1932) and Jordan and Evermann (1896) reported that riverendi had a greater body depth than variegatus. South Florida populations do not differ greatly from adjacent populations to the north and could not be allied with riverendi on the basis of this character. The relationship between reduced body depth and decreased salinity is not supported in the literature for Cyprinodon. Chipman (1958) noted no salinity influence on this character and Sweet and Kinne (1964) reported greater body depth with decreased salinity in newly hatched C. macularius. Reduced salinity appears to separate freshwater populations from other Cyprinodon populations better in the males than females. This is especially true with hubbsi.

Body Width (Figure 7, Table 15). Along the west coast, body width appears to increase irregularly to about the vicinity of Levy County, then decrease along the coast to south Florida. An increase in width occurs north along the east coast and a slight, irregular trend appears to exist with body width increasing from the west to east coast. A possible reduction of body width at lower salinities is noted among some populations.

Caudal Peduncle Depth (Figure 8, Table 16). Caudal peduncle depth population means decrease both north and south of Levy County on the west coast, but no geographical pattern is evident for the east coast. Lowest average depths are shown for the population of hubbsi; however, a significant salinity effect is noted. All freshwater collections have lower peduncle depths than other adjacent coastal populations.

FIGURE 7

Body width expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

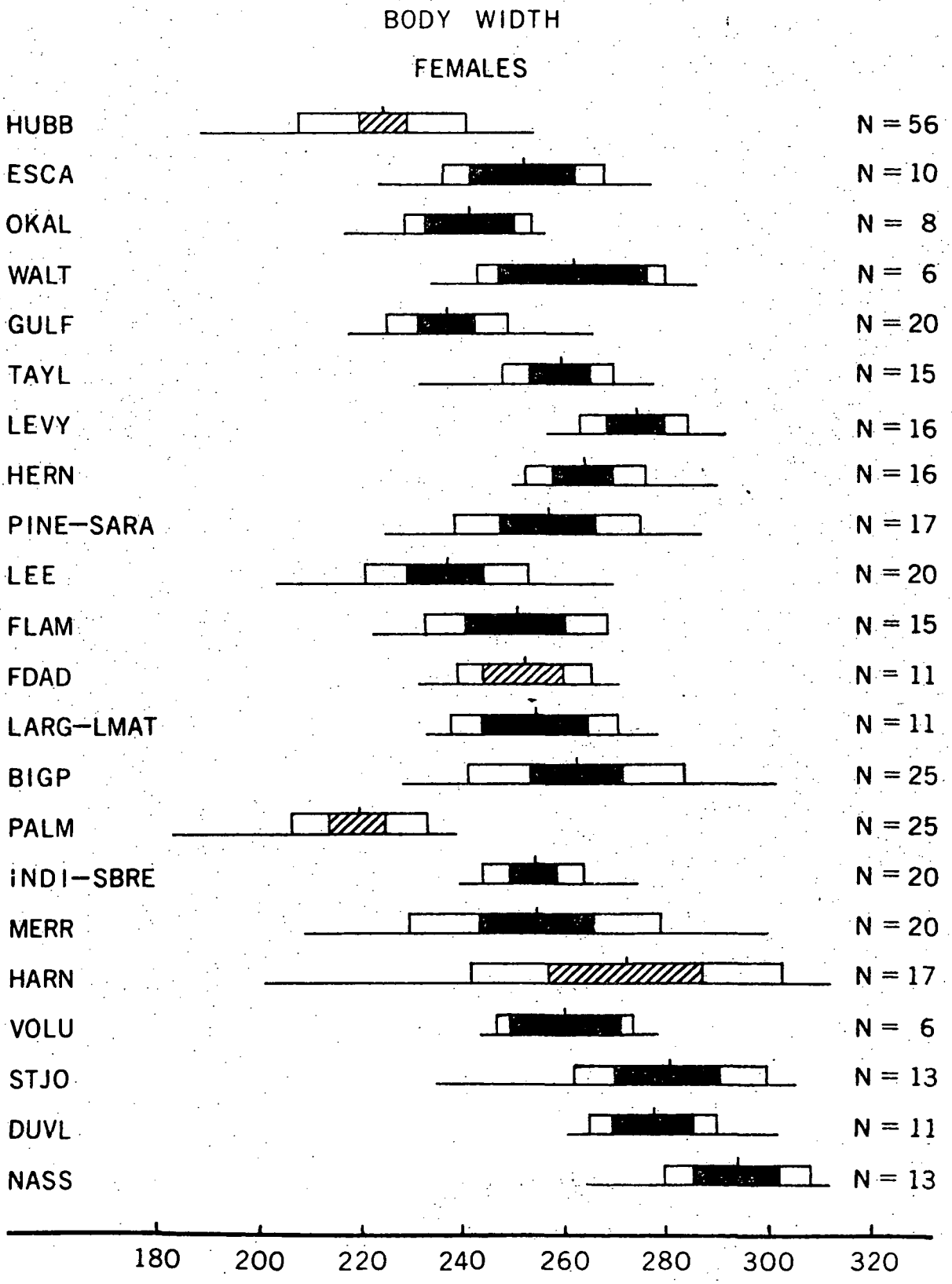
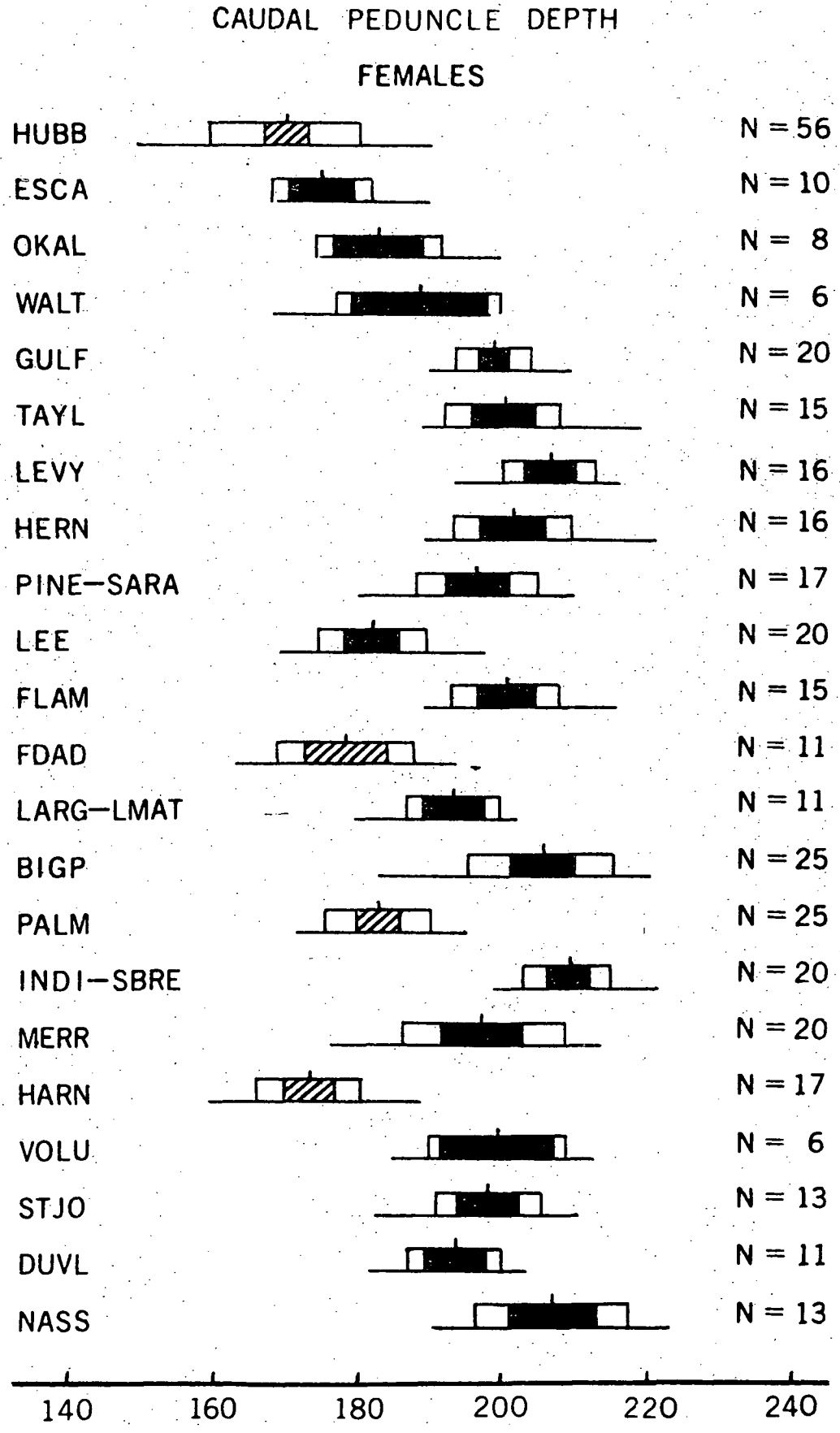

BODY WIDTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
180
200
220
240
260
280
300
320

FIGURE 8

Caudal peduncle depth expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


CAUDAL PEDUNCLE DEPTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
140
160
180
200
220
240

Predorsal Length (Figure 9, Table 17). No environmental influence of this character on population means by temperature or salinity is observed, even though hubbsi has slightly lower predorsal lengths than other Florida Cyprinodon. Lack of environmental influences on this character was noted by Chipman (1958). The data indicate a slight, irregular trend of increasing predorsal length south along the west coast to Hernando County.

Dorsal Origin to Caudal Base (Figure 10, Table 18). This character appears to decrease both north and south of Levy County on the west coast while values from the east coast generally decrease northward. The lower means for freshwater populations suggest that this character is affected by variations in salinity.

Prepectoral Length (Table 19). Freshwater populations have lower average prepectoral lengths than adjacent coastal populations. Highest values are found in Levy County on the west coast. Except for Nassau County, a decreasing south-to north pattern is noted among populations from the east coast. A possible temperature effect may exist for this character since lowest values are generally present in the northern sections of the Florida coasts.

Anal Origin to Caudal Base (Figures 11 and 12, Table 20). This measurement is quite variable among freshwater populations and any salinity influence on the character is obscure. Populations of hubbsi exhibit the highest values for males and nearly so for females. This character, better than any other, separates hubbsi from other Florida populations without having to consider possible effects caused by salinities. A slight decrease in the anal origin to caudal base lengths is evident southward along the west coast.

FIGURE 9

Predorsal length expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

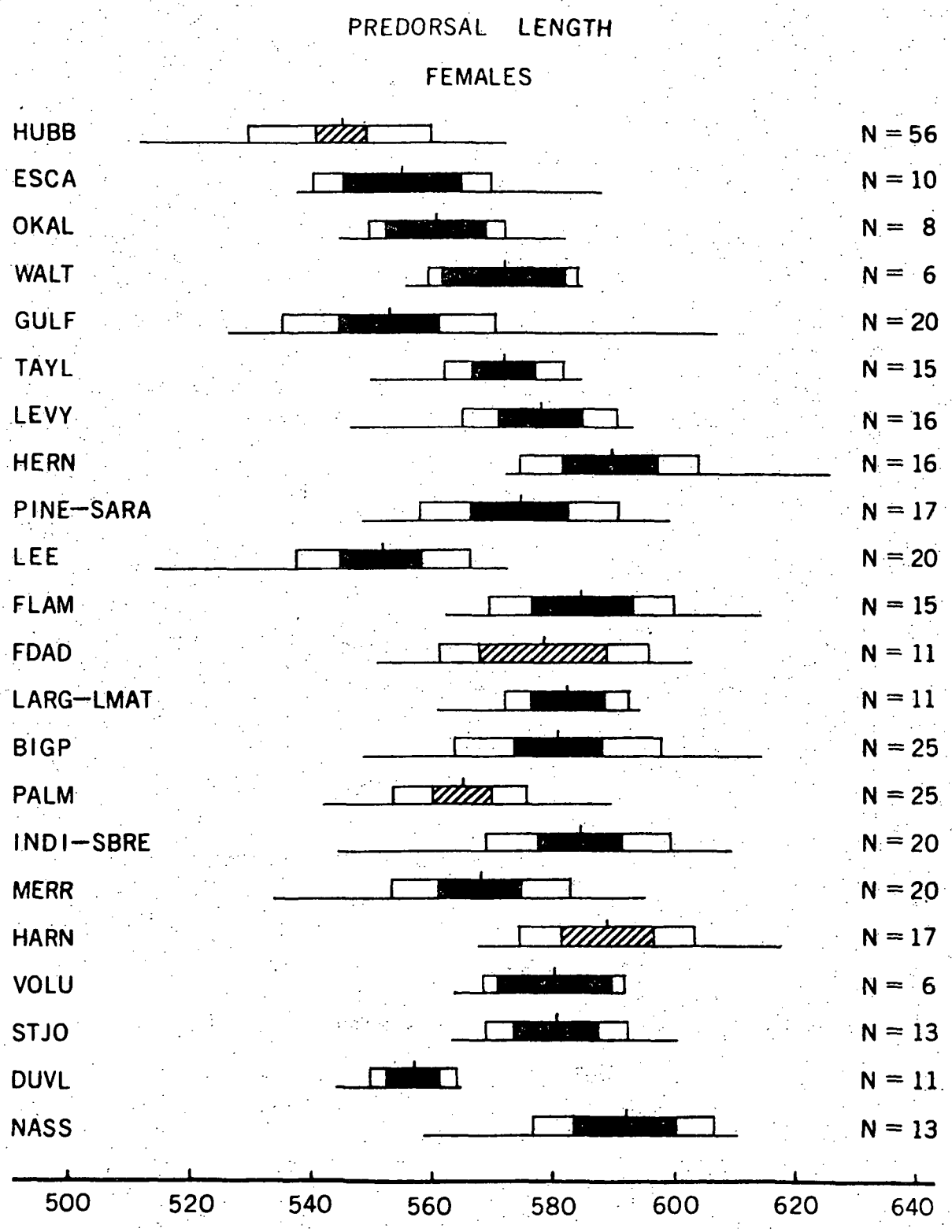

PREDORSAL LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
500
520
540
560
580
600
620
640

FIGURE 10

Dorsal origin to caudal base expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

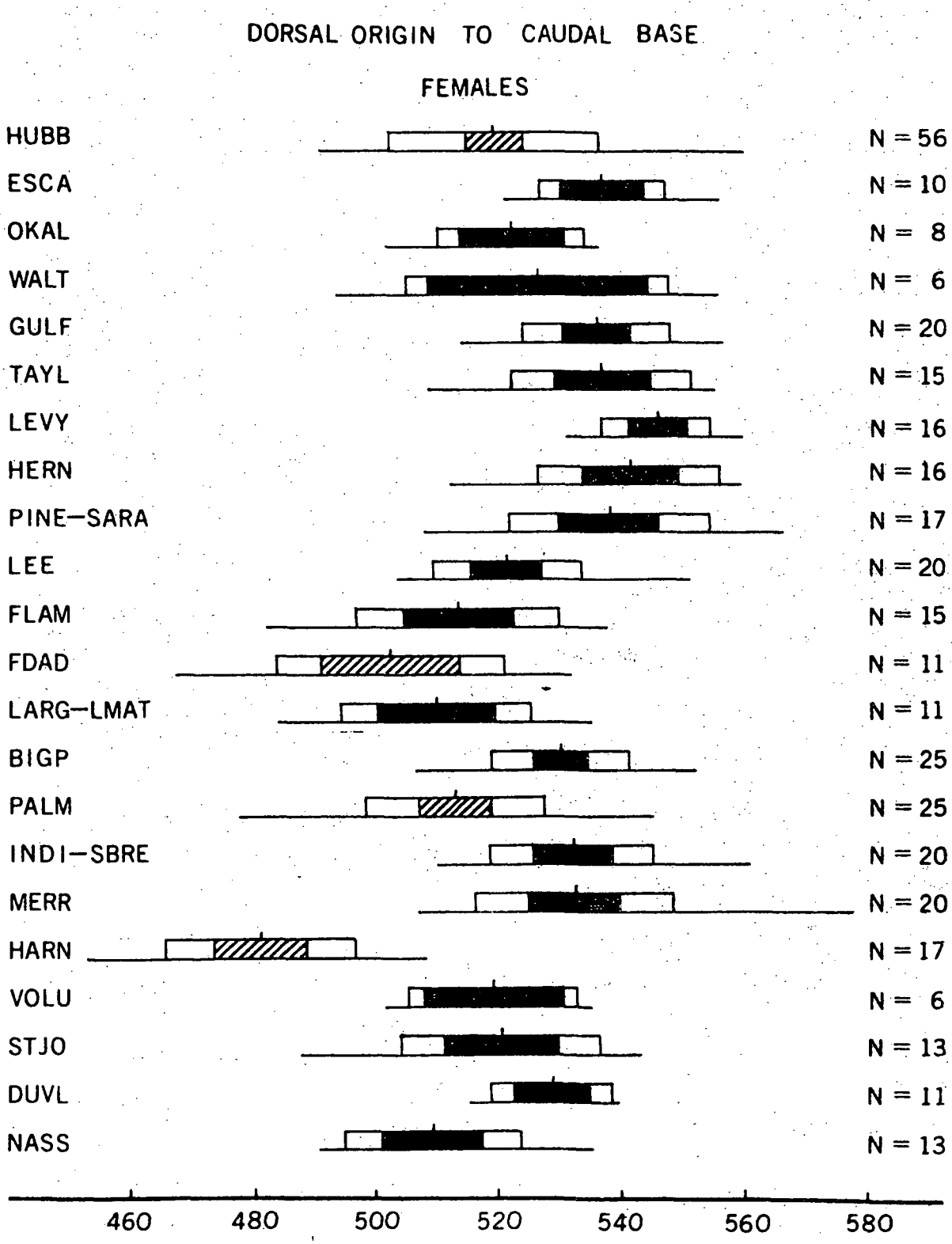

DORSAL ORIGIN TO CAUDAL BASE
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
460
480
500
520
540
560
580

FIGURE 11

Anal origin to caudal base expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

ANAL ORIGIN TO CAUDAL BASE

FEMALES

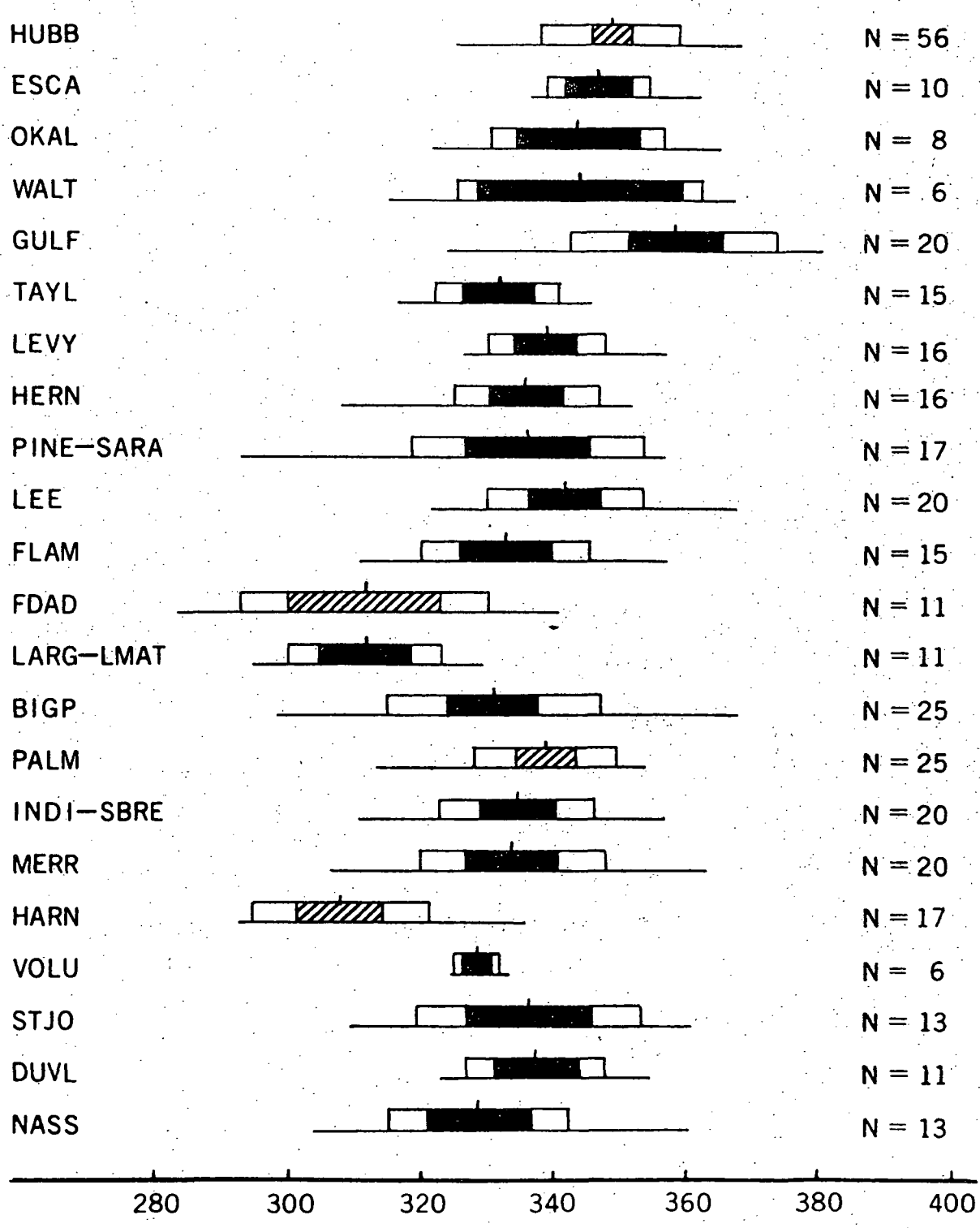
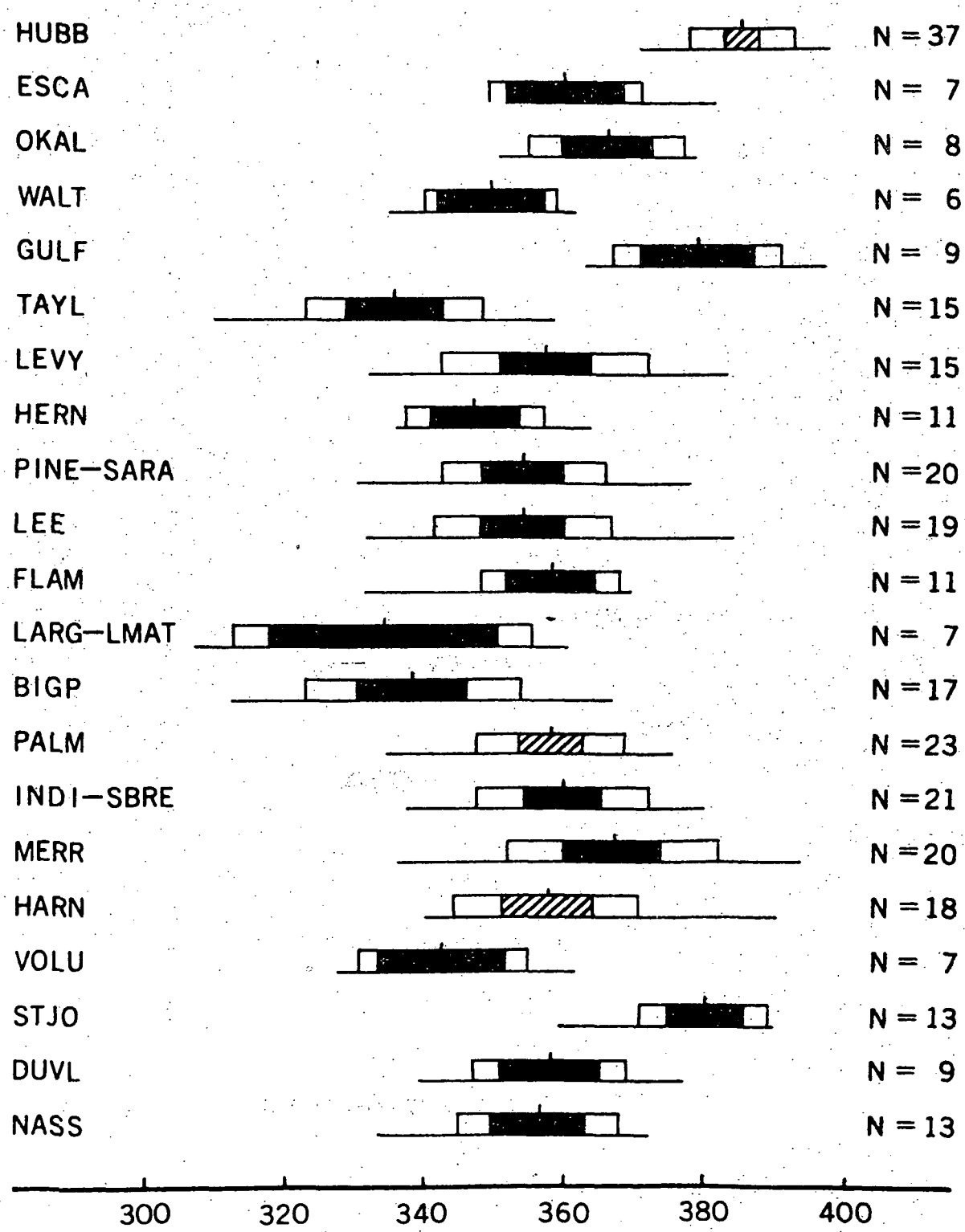


FIGURE 12

Anal origin to caudal base expressed as thousandths of standard length for males of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

ANAL ORIGIN TO CAUDAL BASE

MALES



Pectoral Origin to Dorsal Origin (Table 21). These data show approximately the same geographical patterns as those for body depth. Highest values are found on the west coast at Levy County. The lowest population average is found in the hubbsi collection, but other freshwater populations also demonstrate a tendency toward low values.

Pelvic Length (Figure 13, Table 22). Mean values for this character generally appear to increase southward along the coast to Sarasota County in the west and Indian River County in the east. South of these areas the pelvic fins are generally reduced in length, the only exception being at Big Pine Key. The coastal pattern of population means imply that decreased length of pelvic fins is associated with reduced temperatures in the north. A possible reduction in fin lengths is suggested for freshwater populations.

Head Length (Figure 14, Table 23). The data suggest a general increase in head length south along both coasts as far as Flamingo on the west and to Palm Beach County on the east. More southerly populations have slightly lower values, not in keeping with this trend. Jordan (1884) stated that riverendi from the Keys have smaller heads than variegatus. If this group proves to be riverendi, this statement could be true with respect to adjacent northern populations. These coastal patterns also imply increased higher water temperatures may increase the head lengths of coastal Cyprinodon in South Florida. Desert Cyprinodon from warm springs have been shown to have larger heads than those from cooler waters (Miller, 1948). Figure 14 shows the effect of reduced salinity on head length. Freshwater populations are shown to have lower average head lengths than those from coastal areas.

FIGURE 13

Pelvic fin length expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

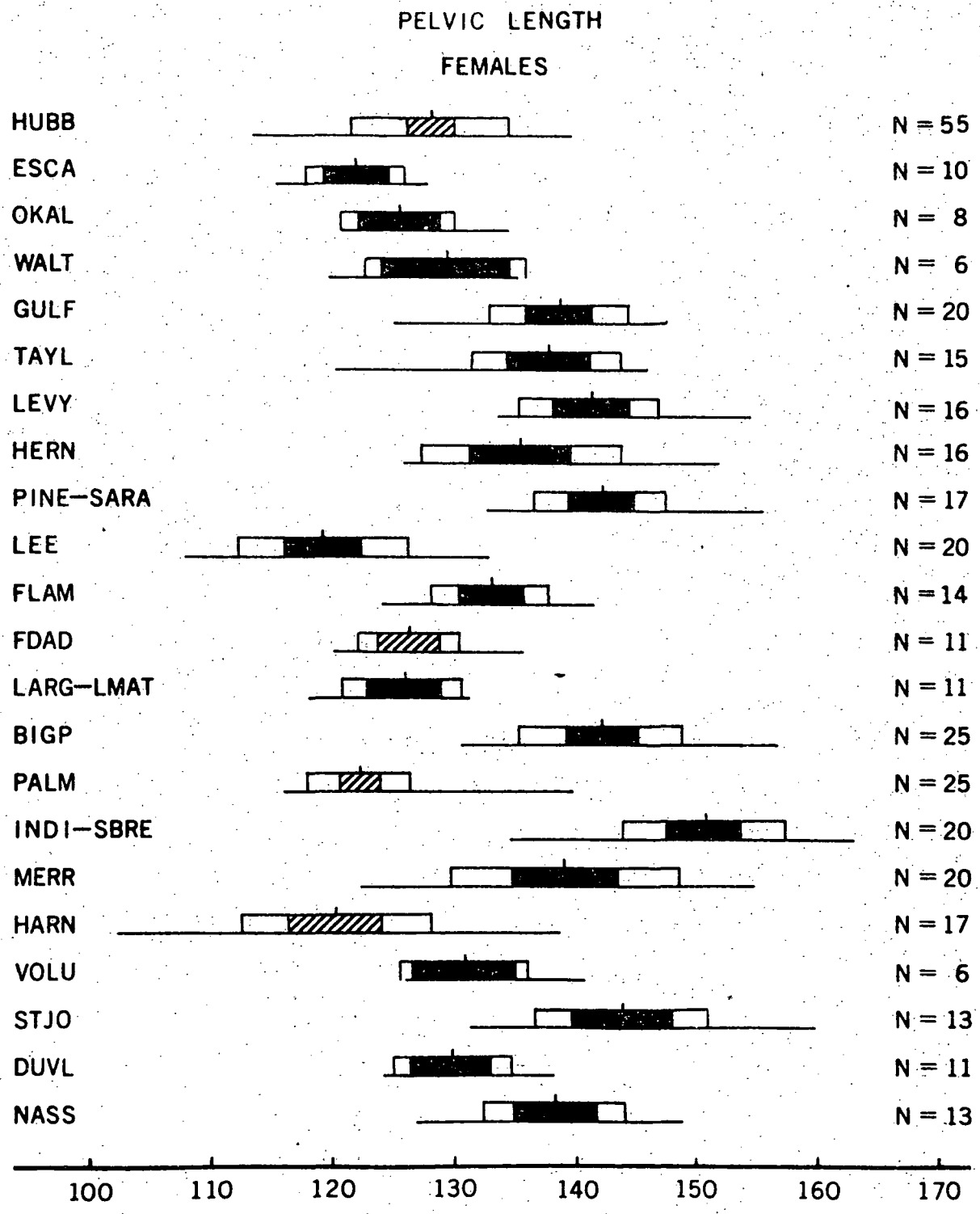
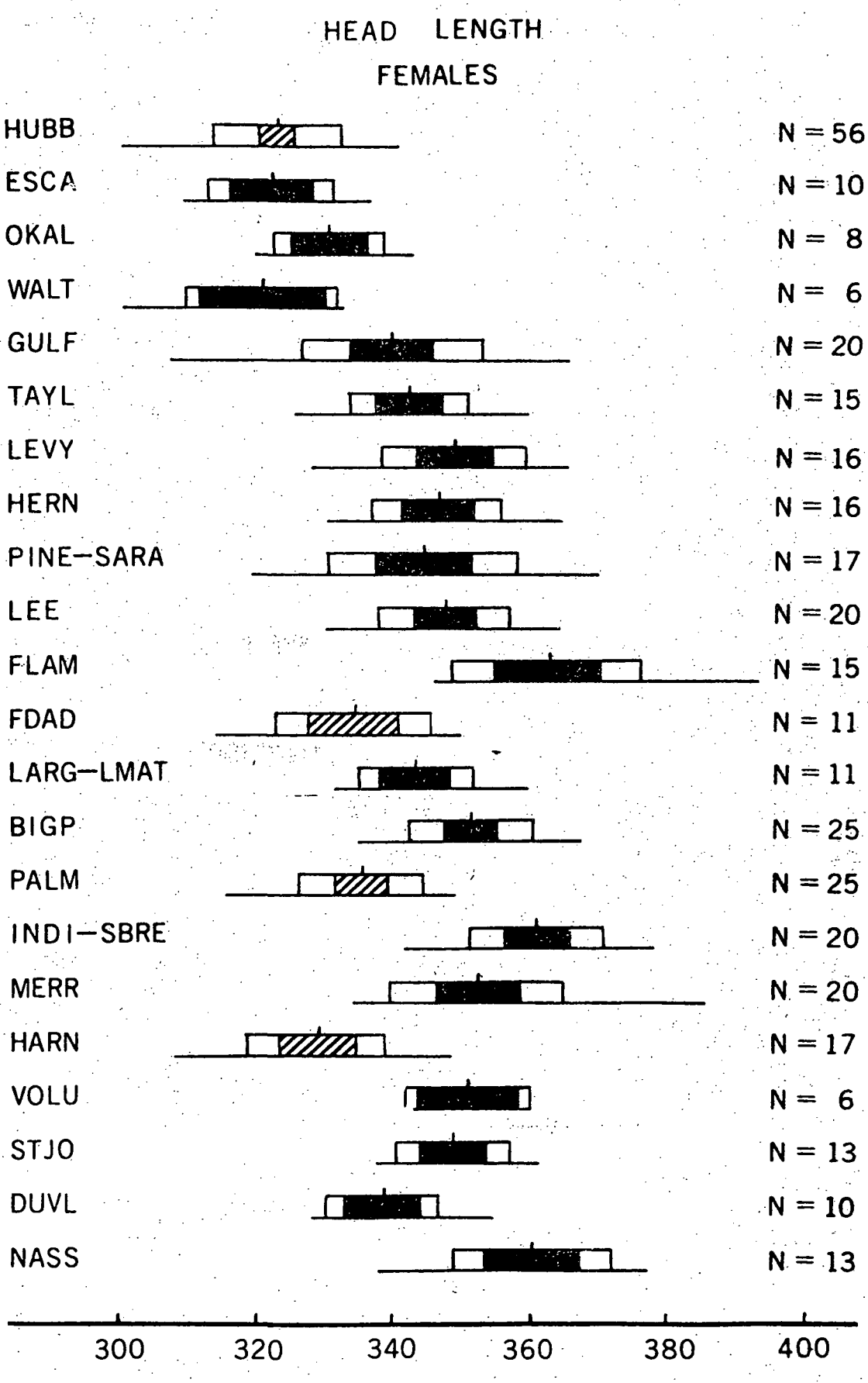

PELVIC LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 55
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 14
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 11
N = 13
100
110
120
130
140
150
160
170

FIGURE 14

Head length expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


HEAD LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 10
N = 13
300
320
340
360
380
400

Head Depth (Figures 15 and 16, Table 24). Flatter heads and lesser head depths have been reported for both hubbsi and artifrons (Carr, 1936a; and Hubbs, 1936). Hubbs (1936) reported that artifrons had a lesser head depth than the subspecies ovinus. Maximum values for Florida Cyprinodon populations are found in Levy County on the west coast, and east coast populations tend to decrease northward, except for Nassau County. Populations from the northwest coast have lesser head depths than those from the northeast coast and an overall irregular trend of this type is observed. Although hubbsi has an average head depth lower than any other Cyprinodon population, especially in the males, all freshwater groups appear to have low head depth values. Chipman (1958) noted no salinity effect on head depth.

Snout Length (Table 25). Snout length is so consistent among populations that no visual correlations are noted with respect to geography, salinity or temperature.

Cheek Height (Table 26). Because of the variability of this character among populations, no geographical patterns can be observed within Florida. No relation with salinity is noted. An ontogenetic change of increased percent of standard length with increased growth within the size range of 25-51 mm SL has been noted by Gilmore and Williams (unpublished manuscript). Thus this character may be of little taxonomic value.

Postorbital Length of Head (Figure 17, Table 27). Two major patterns among population means of postorbital head length exist within Florida Cyprinodon. A definite decrease in mean values of

FIGURE 15

Head depth expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

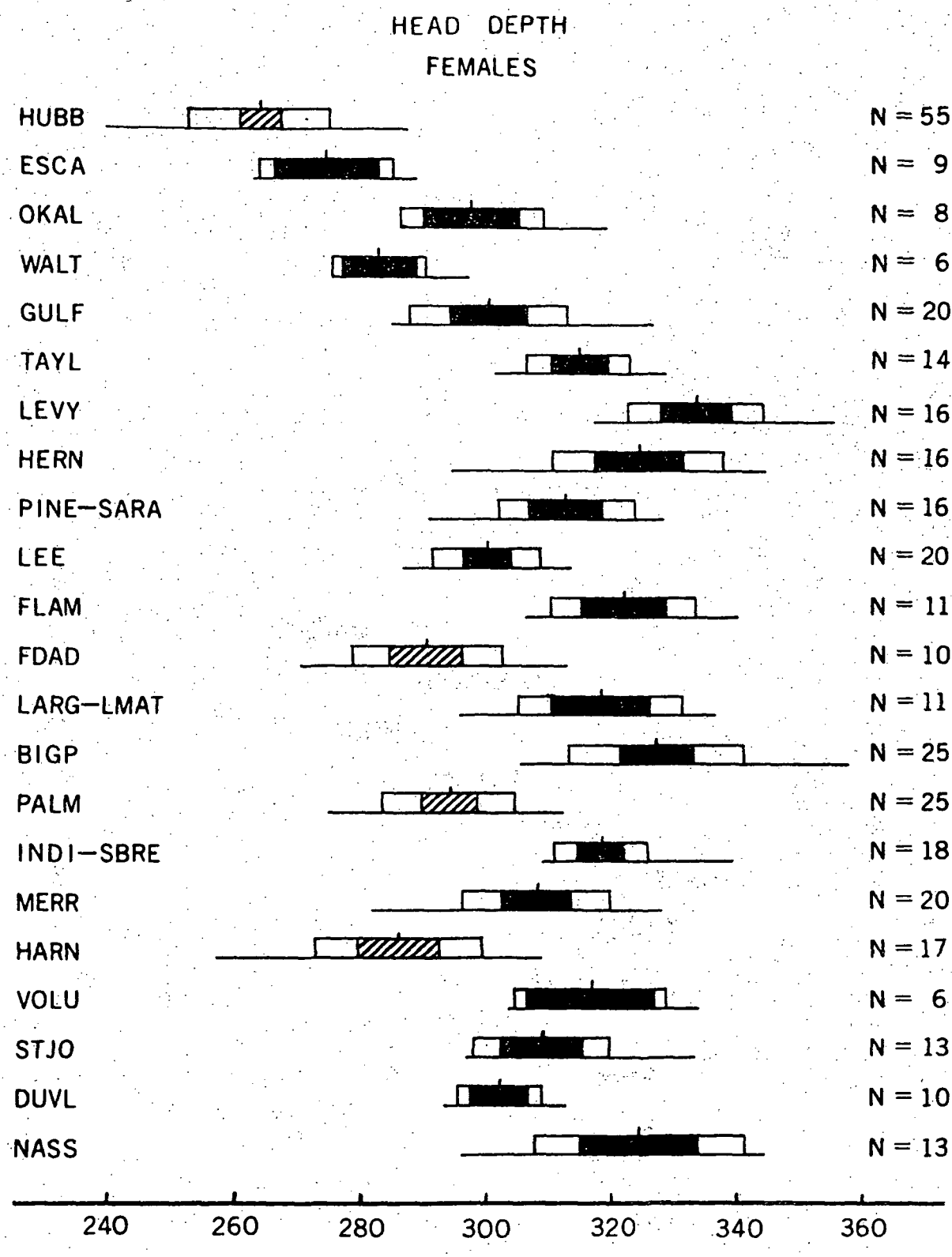

HEAD DEPTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 55
N = 9
N = 8
N = 6
N = 20
N = 14
N = 16
N = 16
N = 16
N = 20
N = 11
N = 10
N = 11
N = 25
N = 25
N = 18
N = 20
N = 17
N = 6
N = 13
N = 10
N = 13
240
260
280
300
320
340
360

FIGURE 16

Head depth expressed as thousandths of standard length for males of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

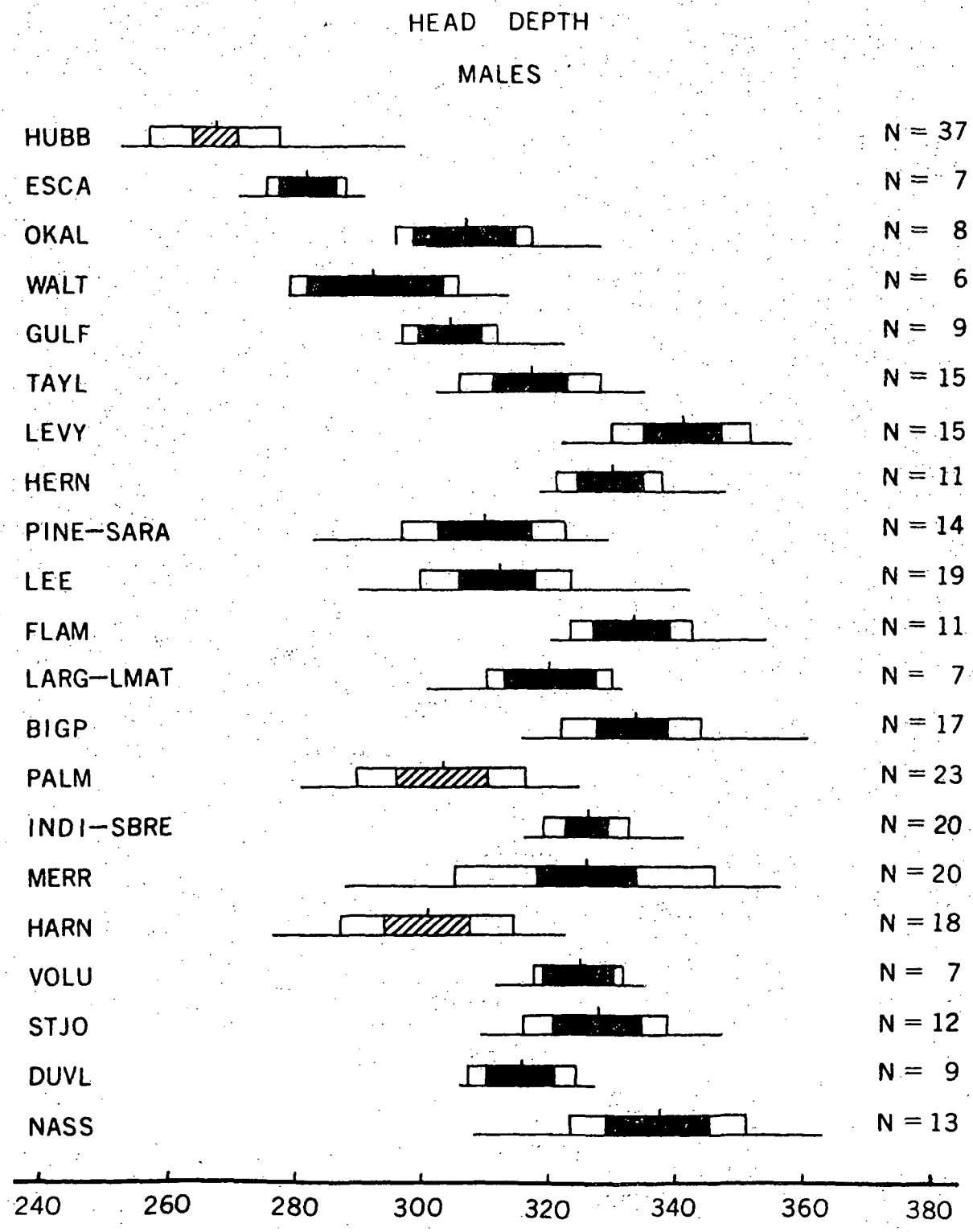
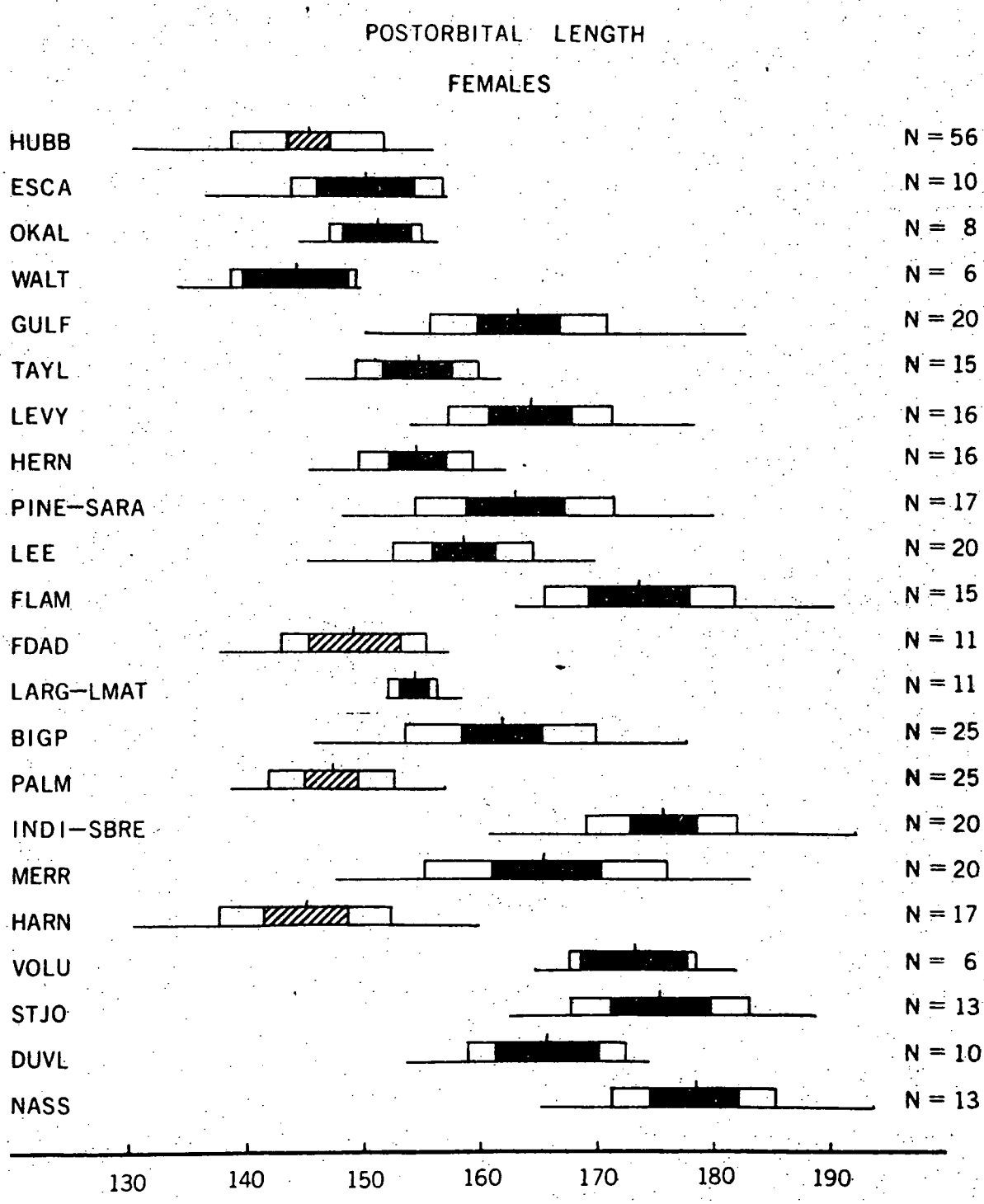

HEAD DEPTH
MALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 37
N = 7
N = 8
N = 6
N = 9
N = 15
N = 15
N = 11
N = 14
N = 19
N = 11
N = 7
N = 17
N = 23
N = 20
N = 20
N = 18
N = 7
N = 12
N = 9
N = 13
240
260
280
300
320
340
360
380

FIGURE 17

Postorbital length of head expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


POSTORBITAL LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 10
N = 13
130
140
150
160
170
180
190

postorbital length in freshwater populations is indicated, and a clinal increase in values southward on the west coast and northward on the east coast is apparent.

Interorbital Bony Width (Figure 18, Table 28). Interorbital bony width was used as a major diagnostic character by Carr (1936a) for the separation of hubbsi and variegatus. Populations of hubbsi were reported to have interorbital widths much less than those of variegatus. Although hubbsi does have the least interorbital width of any Florida Cyprinodon population, other freshwater populations show parallel trends when compared with neighboring coastal populations. Figure 18 suggests a geographical trend with maximum values on the west coast at Levy County and an increase in width north along the east coast.

Orbit Length (Figure 19, Table 29). The data indicate a slight overall increase in orbit length south along both coasts to the Florida Keys. However, this increase appears to be much more rapid on the east coast, resulting in much lower values in the north. Maximum values for orbit length are found in south Florida, suggesting an increased length with increased water temperature. Miller (1948) reported that desert Cyprinodon from warm springs possessed larger eyes than those from cooler waters.

Orbit to Angle of Preopercle (Figure 20, Table 30). The figures reveal an irregular increase in the orbit to angle of preopercle length southward along the west coast and northward on the east coast. Populations of hubbsi have values lower than most other populations but other freshwater groups do not exhibit average values much less than their adjacent populations.

FIGURE 18

Interorbital bony width expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

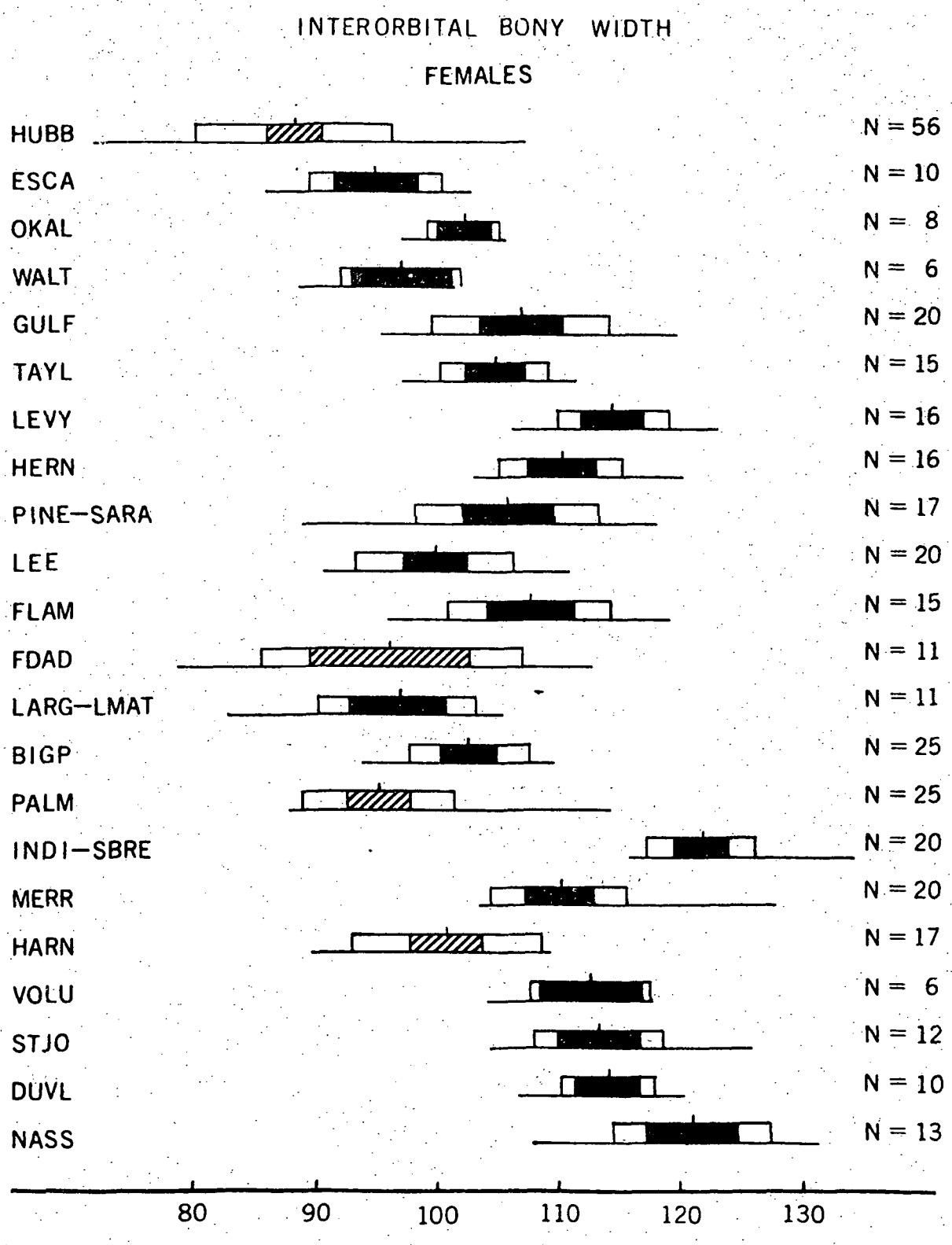

INTERORBITAL BONY WIDTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE—SARA
LEE
FLAM
FDAD
LARG—LMAT
BIGP
PALM
INDI—SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 12
N = 10
N = 13
80
90
100
110
120
130

FIGURE 19

Orbit length expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

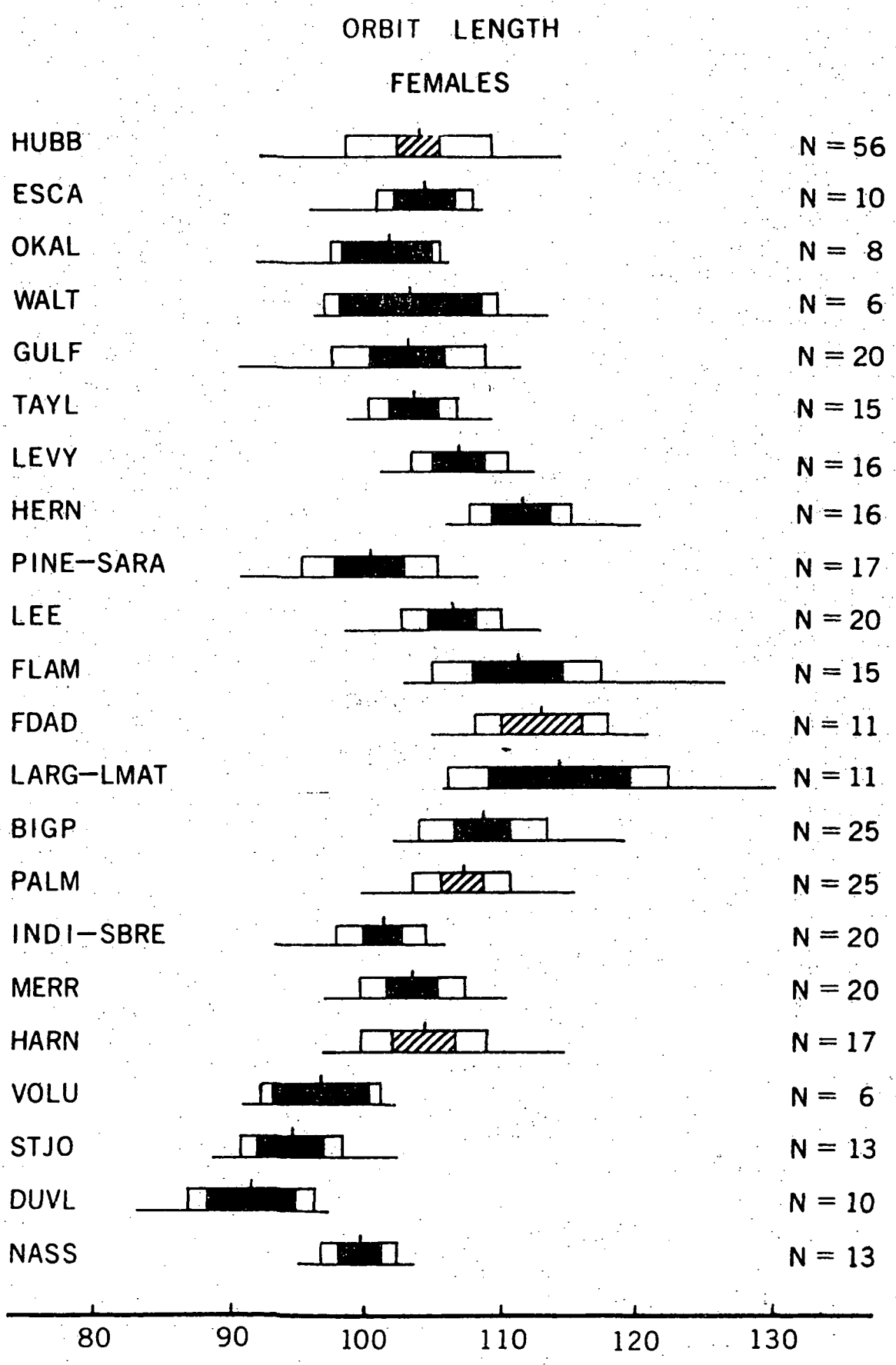
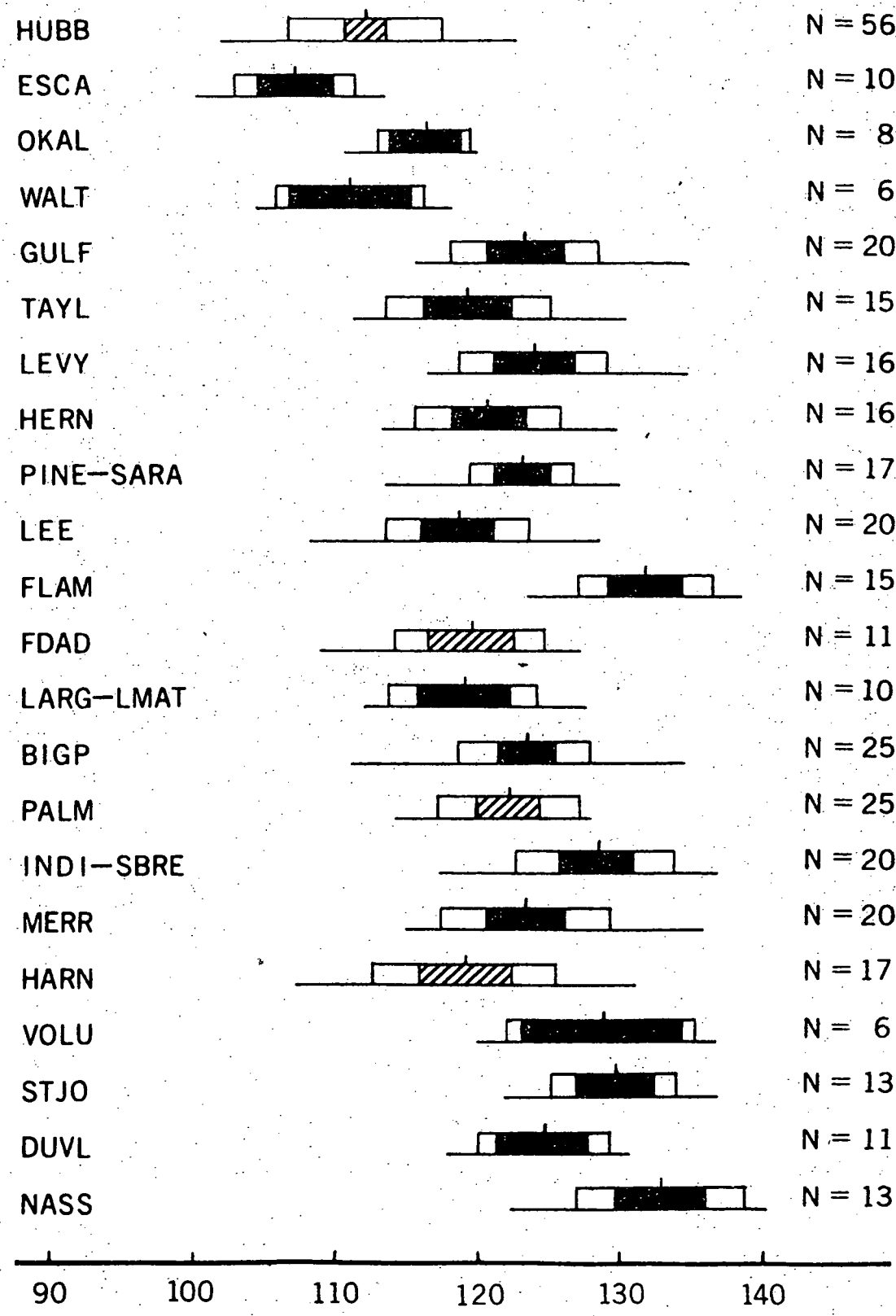

ORBIT LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 10
N = 13
80
90
100
110
120
130

FIGURE 20

Orbit to angle of preopercle expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

ORBIT TO ANGLE OF PREOPERCLE

FEMALES



Opercle Length (Figure 21, Table 31). The data demonstrate the presence of reduced opercle lengths among freshwater populations. The presence of an irregularly increasing cline, south along the west coast and north on the east coast is noted. No effect on opercle length by temperature is apparent.

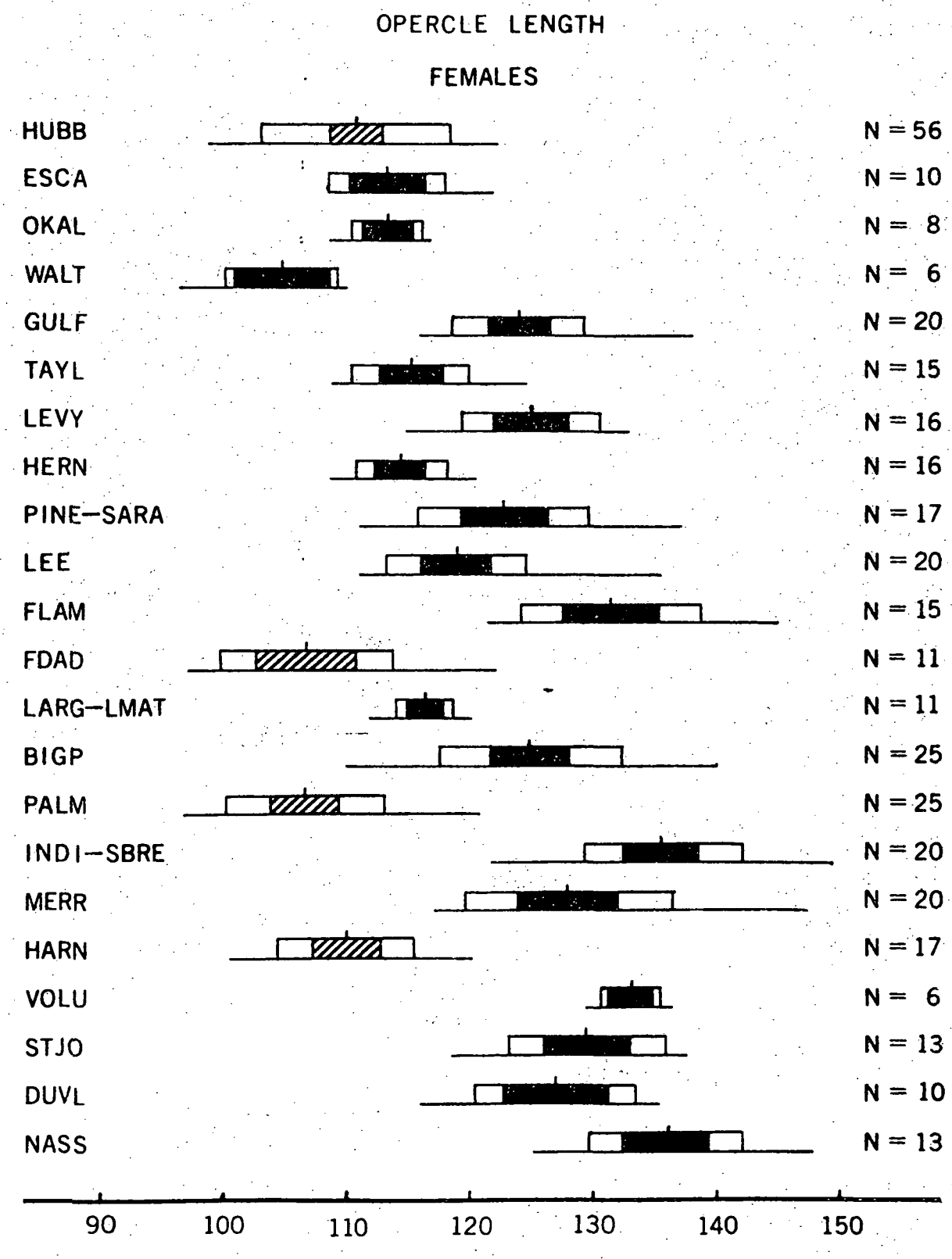
Sexual Dimorphism

Sexual dimorphism is marked in the genus Cyprinodon. A table of pigmentation characteristics of male and female Cyprinodon variegatus is given by Raney et al., (1953).

A summary of sexual dimorphism in measurements for variegatus and hubbsi in Florida is present in Table 32. No differences are apparent between the sexes in the meristic characters studied. Considerable sexual dimorphism exists, however, in a number of the morphometric characters analyzed. The student's t statistic showed that significant sexual dimorphism (P less than .05) exists in the following characters: body depth (Table 14), body width (Table 15), caudal peduncle depth (Table 16), predorsal length (Table 17), dorsal origin to caudal base (Table 18), anal origin to caudal base (Table 20), pectoral origin to dorsal origin (Table 21), pelvic length (Table 22), head depth (Table 24) cheek height (Table 26), interorbital bony width (Table 28), orbit length (Table 29), and orbit to angle of preopercle (Table 30). No difference between the sexes was observed for prepectoral length (Table 19), head length (Table 23), snout length (Table 25), postorbital head length (Table 27), and opercle length (Table 31). For all characters examined the mean value of the males was greater in every case except in body width and predorsal

FIGURE 21

Opercle length expressed as thousandths of standard length for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.


OPERCLE LENGTH
FEMALES
HUBB
ESCA
OKAL
WALT
GULF
TAYL
LEVY
HERN
PINE–SARA
LEE
FLAM
FDAD
LARG–LMAT
BIGP
PALM
INDI–SBRE
MERR
HARN
VOLU
STJO
DUVL
NASS
N = 56
N = 10
N = 8
N = 6
N = 20
N = 15
N = 16
N = 16
N = 17
N = 20
N = 15
N = 11
N = 11
N = 25
N = 25
N = 20
N = 20
N = 17
N = 6
N = 13
N = 10
N = 13
90
100
110
120
130
140
150

length. A greater body width in females is probably attributed to the presence of gravid females in some of the collections examined. Whenever possible, females with obviously distended abdomens were not selected for study. Chipman (1958) also noted that females had greater body widths and slightly greater predorsal lengths but otherwise he reported significant sexual dimorphism to exist only in dorsal, anal and pectoral fin lengths and head depth.

As seen in Table 32, hubbsi differs from variegatus in that no significant sexual dimorphism exists in depth measurements of body depth, dorsal origin to pectoral origin, and head depth; or for cheek height, interorbital bony width, or orbit to angle of preopercle.

Characters of Cyprinodon from Oklawaha Lakes

Variation exists in meristic and morphometric characters of Cyprinodon populations among the various lakes at the headwaters of the Oklawaha River. Many of these variations are correlated with productivity and/or salinity. Characteristics of these lakes are shown in Table 33. The lakes are arranged in this table according to increasing productivity. Brezonik et al., (1969) have correlated most major ions with productivity. Of all the constituents which show significant variation among the lakes, only Na and Cl ion concentrations do not parallel the pattern of increasing productivity.

Populations of hubbsi examined in this study are from lakes Weir, Harris, Eustis, and Dora, at the headwaters of the Oklawaha River. All meristic and morphometric characters studied are shown in Tables 34 through 44 for these four lakes. In addition, results of some

meristic characters are given for lakes Yale and Griffin. Only juvenile specimens were available from these two lakes.

Results of an analysis of variance performed on meristic characters indicated that the means of most are not equal among the lakes inhabited by hubbsi. Among meristic characters, the means are equal (P greater than .05) for dorsal, anal, and caudal fin rays (Table 34), predorsal scales (Table 35), dorsal origin to anal origin scales (Table 36), suborbital scales (Table 37), and frontal scales. The means are not equal among these lakes (P less than .001) for lateral scales (Table 35), belly to dorsal origin scales (Table 35), dorsal origin to pelvic origin scales (Table 36), and circumference scales (Table 37). For morphometric characters, means are equal for the length of the pelvic fin (Table 41), and opercle length (Table 44) for the females, and prepectoral length (Table 40), anal origin to caudal base (Table 40), pelvic fin length (Table 41), and post-orbital head length (Table 42) in males. The means for all other characters shown in Tables 38 through 44, for both males and females, are not equal among the lakes.

In these lakes, a relationship exists among most characters with unequal means with respect to either variations in salinity or productivity. Among characters with unequal means, an increase in mean values from lakes with relatively low productivity (Weir and Harris) to those with high productivity (Eustis and Dora) is indicated for the depth measurements of body depth (Table 38), caudal peduncle depth (Table 39), head depth (Table 41), and pectoral origin to dorsal origin (Table 40). In addition to these characters, this pattern

seems to exist with body width (Table 38) and belly scales (Table 36), and all body circumference scale counts (Belly to dorsal origin, dorsal origin to pelvic origin, and circumference scales). The converse of this trend may exist for orbit length (Table 43).

The depth measurements and body circumference scale counts are the primary characters distinguishing hubbsi from other Florida populations. Kinne (1966) has demonstrated that C. macularius inhabiting fresh water show significant reduction of gross efficiency of converting food into body substances. If food is limiting to the degree at which it affects the ecological potential of the fish, an environmental effect on these characters could be possible.

One other pattern of character variation with respect to environment possibly exists in the Oklawaha lakes. As shown in Table 33, Na and Cl ions do not follow the trend of the other constituents with productivity. With respect to these two ions, Lakes Harris and Eustis are low in concentration and Dora and Weir are high. Although the concentration of these ions is low as compared to coastal waters, many characters of unequal means seem to correlate with this trend. Average proportional measurements of predorsal length (Table 39), head length (Table 41), snout length (Table 42), cheek height (Table 42), postorbital length (Table 42), interorbital widths (Table 43), and orbit to angle of preopercle (Table 44) have low values for Harris and Eustis and high values for Dora and Weir. A converse trend with salinity is evident for dorsal origin to caudal base length (Table 39) and lateral scales (Table 35).

Whether or not these trends are due to salinity, productivity, or other environmental factors, or are purely genetic is not immediately

evident. The effects of environmental factors on morphological variation are discussed later.

The Effects of Environmental Factors on Morphological Variation

Since it has been shown that Cyprinodon may tolerate wide fluctuations within its normal habitat, the possible effects of temperature and salinity on meristic and morphometric characters must be considered. Miller (1948) stated that relationships exist between characters and the environment indicating the interrelationship of genetic, salinity and temperature controlled factors. Kinne and Kinne (1962a,b) have shown that temperature, salinity and oxygen may greatly affect the rate and efficiency of embryonic development in C. macularius. The influence of the environment on structural characters must be understood so that genetic differences that may exist among populations are not obscured.

Miller (1948, 1950) suggested a relationship between high environmental temperatures and a decrease in the number of scales and rays, and noted that this probably was a result of accelerated growth in early stages of development. "Although no definite correlation between temperature and meristic characters can be demonstrated when comparing distinct populations within one area or between two regions, a general correlation of this nature is evident" (Miller, 1948:134). A correlation does, however, exist between temperature and various meristic characters within a single population of desert Cyprinodon. This was illustrated by circumference scales, which were fewer in number at cooler spring outlets than at the spring source (Miller, 1948, 1950).

Miller (1948, 1950) demonstrated that temperature played an important role in determining the structure and rate of speciation in Cyprinodon. At a salinity of 35 ppt, the length at hatching of C. macularius decreased with increased temperature in the range of 28-35°C (Kinne and Kinne, 1962a,b). Desert pupfish from warm springs tend to have their dorsal fin positioned more posteriorly, a deeper body, more expansive fins, enlarged head and eye, enlarged anterior body parts, and tend to be smaller (Miller, 1948).

The morphometric characters of newly hatched C. macularius may be significantly altered by temperature variations. In fresh water the body tended to become deeper and wider at temperatures above and below 32-33°C, while the body length decreased. At salinities of 35 and 70 ppt body length decreased with higher temperatures while depth and width dimensions changed proportionally (Sweet and Kinne, 1964).

Miller (1948, 1950) reported that increasing salinity had the same effect on desert Cyprinodon species as decreasing temperatures, that is, an increase in the meristic characters, particularly scale counts. He has also shown a reduction in scale counts of C. nevadensis hatched and raised in waters of reduced salinity. This was especially evident in the scales around the body. Miller (1948) stated that a causal relationship may exist between a decrease in salinity and a decrease in the number of predorsal and body scales. LaBounty and Deacon (1972) elaborated on the relationship between salinity and meristic characters in desert pupfish. With an increase in habitat salinity, an increase in mean values was evident in the number of

dorsal to pelvic scales, dorsal to anal scales, caudal peduncle scales, lateral scales, and predorsal scales, while decreased values were noted for dorsal, anal, pectoral, and caudal rays. No trends were evident with gill rakers, pelvic rays, preopercular pores or preorbital pores. Chipman (1958) also found that lateral scales and predorsal scales of C. variegatus increased with increased salinity. His results differed from LaBounty and Deacon (1972) in that anal and pectoral rays also increased with an increasing salinity. Chipman (1958) found no trends with respect to body scales.

Salinity is also known to influence variation in morphometric characters. Chipman (1958) found that in Cyprinodon variegatus the pectoral fin length and dorsal fin height of males increased with an increase in salinity while the anal fin length decreased with increased salinity. No relationship between body morphology and salinity was noted. Chipman's results are questionable, however, since many of his contrasting fresh and saline water stations were from different ends of the same lake. It seems that the fish could have moved freely among sampling stations.

Sweet and Kinne (1964) demonstrated that variations in salinity during incubation could significantly modify morphological characters of newly hatched C. macularius. Their results showed that body depth and width tended to increase with decreasing salinity, resulting in a rounder fish. Body length, depth, and width were significantly smaller in 70 ppt than in fresh water or 35 ppt. These data are from newly hatched fish, and these trends may have been different if the fish were allowed to mature.

An increase in salinity, particularly above 35 ppt, leads to increased retardation of development. However, this decrease has been found to be relatively small over the salinity range from 0-35 ppt. The hatching length of C. macularius decreases with an increase in salinity from 18 to 70 ppt (Kinne and Kinne, 1962a,b).

Kinne (1966) has shown that variations in salinity (fresh water, 15 ppt, and 35 ppt) result in significant differences in gross efficiency of food conversion into body substances for C. macularius kept at 30°C. Efficiency of growth was maximized at 15 ppt and minimized in fresh water. These changes may greatly affect ecological potential (Kinne, 1966) and in that fish living at salinities other than that of maximum efficiency of food conversion may be under some stress. In general, populations of Cyprinodon living under conditions of environmental stress have a larger proportion of smaller individuals (LaBounty, 1968). Chipman (1958) also noted that C. variegatus from more saline environments had larger average standard lengths. Cyprinodon from the headwaters of the Oklawaha River are decidedly smaller than estuarine populations (Carr, 1936a). The data of Renfro (1960) and Gunter (1945), however, showed no relationship between fish size and the salinity in the area of their capture.

Miller (1950:161) stated that a direct, environmental influence was indicated for the morphological variations among populations of desert Cyprinodon, "but it is thought that the observed differences are due in part to genetic adaptations that parallel those due to the direct effect of the surroundings." Among pupfish studied by LaBounty (1968), those species from the most saline environments

generally had the higher scale counts while C. milleri, from the least saline habitat, had the lowest scale counts (except lateral scales). Thus it is apparent that salinity has an important influence on the differentiation among species of Death Valley Cyprinodon. However, LaBounty (1968:100) noted that the primary characters used to distinguish the various species have some relationship to salinity differences and that the validity of some species in the Death Valley system was open to question. He concluded, however, that C. milleri was "as distinct and therefore as legitimately recognizable as other species in the System."

In experiments conducted by Miller (1950) on various subspecies of desert Cyprinodon, meristic characters of F_1 hybrids retained their respective identity, with a few exceptions, regardless of the salinity at which they were raised. Thus he felt that heredity, as well as environment, influenced the meristic and morphological differences among Cyprinodon populations.

The rate of speciation of Death Valley Cyprinodon species is also influenced by salinity and temperature. Speciation may be accelerated in these pupfish as a result of high water temperatures and the consequent year-around breeding and short generation times (Miller, 1948, 1950). A continuous river was present in Death Valley about 4000 years ago, permitting uninterrupted gene flow throughout the area where the populations of C. salinus, C. milleri, and subspecies of C. nevadensis now exist (LaBounty, 1968). Several populations of desert pupfish have evolved fast enough to produce new subspecies within a few hundred to a few thousand years (Miller, 1950).

Within Florida Cyprinodon populations, a relationship between many morphological characters and water temperature is indicated by the data. The existence of character clines which show comparable gradual changes from north to south along both coasts suggests a temperature influence on that character. Circumference scales (Figure 3, Table 6), belly origin to dorsal origin scales (Table 7), dorsal origin to anal origin scales (Table 8), dorsal origin to pelvic origin scales (Table 9), belly scales (Figure 4, Table 10), pelvic fin length (Figure 13, Table 22), and possibly head length (Figure 14, Table 23) all show increasing mean values south along both the east and west coast of Florida. McNulty et al., (1972) have indicated that average temperatures of northern coastal waters are cooler than those of south Florida, especially during the winter.

Changes in morphological characters correlated with variations in salinity are evident within Florida Cyprinodon populations. Freshwater populations which have character means greatly increased or decreased from those of adjacent coastal populations or which are drastically removed from a relatively constant cline are suspected to be influenced by decreased salinity. Since populations of hubbsi at the headwaters of the Oklawaha River inhabit freshwater lakes, special attention was directed toward characters for which hubbsi is differentiated and which also are correlated with low salinity.

Circumference scale counts of belly to dorsal origin (Table 7), dorsal origin to anal origin (Table 8), dorsal origin to pelvic origin (Table 9), and circumference scales (Figure 3, Table 6) all show slightly lower counts in populations inhabiting fresh water.

Body depth (Figures 5 and 6, Table 14), caudal peduncle depth (Figure 8, Table 16), pectoral origin to dorsal origin (Table 21), head depth (Figures 15 and 16, Table 24), prepectoral length (Table 19), head length (Figure 14, Table 26), postorbital head length (Figure 17, Table 27), interorbital width (Figure 18, Table 28), opercle length (Figure 21, Table 31), and possibly dorsal origin to caudal base (Figure 10, Table 18), and pelvic fin length (Figure 13, Table 22) exhibit a relationship of reduced means with decreased salinity. Characters which may be correlated with salinity all appear to have lower means in freshwater populations. The absence of converse trends may indicate that efficiency of growth and thus body proportions are reduced in freshwater Cyprinodon (Kinne, 1966). This may be further supported by populations of hubbsi which show an increase in all depth measurements and circumference scale counts with increasing lake productivity.

No populations of Florida Cyprinodon inhabit environmental situations as extreme as those in the desert. Nevertheless, environmental factors do have an effect on morphological variation. No abnormally accelearated speciation rates are evident for Florida Cyprinodon as a result of extremely high temperatures or salinity. Whether morphological variations noted among Florida Cyprinodon populations are due to environmental factors or are purely genetic is not known. Observed differences are probably, as Miller (1950) states, due to a combination of genetic adaptations that parallel those caused by the environment. Genetic adaptations probably follow those of the environment; however, relatively recent isolation has not permitted morphological differentiation at the specific level.

Geographic Clines

Several consistent patterns of variation are regularly repeated in Florida populations of Cyprinodon variegatus.

Values which increase clinally southward along both coasts, indicating a possible temperature effect are observed for the following characters: belly to dorsal origin scales (Table 7), dorsal origin to anal origin scales (Table 8), dorsal origin to pelvic origin scales (Table 9), belly scales (Figure 4, Table 10) and circumference scales (Figure 3, Table 6). Similar but more irregular clines of this type are suggested for predorsal scales (Table 5), caudal rays (Table 3), and pelvic fin length (Table 22). The presence of a distinct south Florida race occasionally interrupts this type of cline.

A general geographic trend in which values increase southward along the west Florida coast and northward along the east coast has been observed for a number of characters. These clines, although sometimes irregular, are observed for postorbital length (Figure 17, Table 27), orbit to angle of preopercle (Figure 20, Table 30), and opercle length (Figure 21, Table 31). Possible clines of this type are suggested for body width (Figure 7, Table 15), head depth (Figures 15 and 16, Table 24), and predorsal length (Figure 9, Table 17).

In addition to the clines just described, other geographical trends are evident within the boundaries of the east and west Florida coasts. Along the west coast, a trend is shown among many morphometric characters, in which maximum values are found in the vicinity of Levy

County, with population means decreasing both northward and southward. This type of geographical variation is demonstrated by body depth (Figures 5 and 6, Table 14), caudal peduncle depth (Figure 8, Table 16), predorsal length (Figure 9, Table 17), dorsal origin to caudal base (Figure 10, Table 18), prepectoral length (Table 19), pectoral origin to dorsal origin (Table 21), head depth (Figures 15 and 16, Table 24), orbit length (Figure 19, Table 29), and possibly body width (Figure 7, Table 14). These values are not attributed to the relative sizes of the fish studied; the mean value of standard lengths among populations examined from the west coast in no way follows this trend. No explanation for this pattern is known.

Continuous increases or decreases in character means are evident along the west coast. A decrease south along the coast is observed for lateral scales (Figure 2, Table 4) and anal origin to caudal base length (Figures 11 and 12, Table 20). An increasing trend, southward on the west coast is seen for belly scales (Figure 4, Table 10) and all circumference scale counts, along with predorsal length (Figure 9, Table 17), pelvic fin length (Figure 13, Table 22), head length (Figure 14, Table 23), cheek height (Table 26), post-orbital head length (Figure 17, Table 27), orbit length (Figure 19, Table 29), orbit to angle of preopercle (Figure 20, Table 30), and opercle length (Figure 21, Table 31). Many of these characters follow previously described geographic clines.

On the east coast of Florida an increase northward in the means of body width (Figure 7, Table 15), orbit to angle of preopercle (Figure 20, Table 30), and possibly pectoral origin to dorsal origin

(Table 21), and interorbital width (Figure 18, Table 28) is evident. A northward decreasing cline is suggested for lateral (Figure 2, Table 4) and belly scales (Figure 4, Table 10), and all circumference scale counts. This trend is also seen for morphometric characters of dorsal origin to caudal base (Figure 10, Table 18), pelvic fin length (Figure 13, Table 22), orbit length (Figure 19, Table 29), prepectoral (Table 19), and head length (Figure 14, Table 23) except for Nassau County, and possibly cheek height (Table 26). Some of these characters may also follow general clines already discussed. No clines are evident along the east coast for body depth (Figures 5 and 6, Table 14), caudal peduncle depth (Figure 8, Table 16), predorsal length (Figure 9, Table 17), anal origin to caudal base (Figures 11 and 12, Table 20), head depth (Figures 15 and 16, Table 24), postorbital length (Figure 17, Table 27), and opercle length (Figure 21, Table 31).

Cyprinodon variegatus hubbsi

Carr (1936a) distinguished hubbsi from variegatus on the following features: smaller size, generally reduced pigmentation, less elevated contour at the origin of the dorsal fin, shallower body depth, narrower interorbital width, and eleven anal rays. The anal ray count was in error and none of the remaining characters or any combination is sufficient to distinguish hubbsi from all other Florida Cyprinodon populations. Carr's diagnosis does not adequately describe the variation of these characters in hubbsi, nor does it consider that some of these characters may be influenced by environmental parameters.

Local Distribution. This form is found in Lakes Eustis, Harris, Dora, Griffin, Yale, Weir, and Silver Lake of the headwaters of the Oklawaha River. These are the only Cyprinodon populations in Florida which inhabit waters above the level of the Pamlico terrace. The Palm Beach County populations referred to as hubbsi by Christensen (1965) are herein assigned to the south Florida race of C. v. variegatus (see below). South Florida Cyprinodon populations were established on the Pamlico terrace well after those at the headwaters of the Oklawaha. These two areas are well separated geographically and no geological evidence exists which would link them.

Abundance. Within its preferred habitat hubbsi is relatively numerous. Although Carr (1936a) collected only 94 specimens from Lake Eustis over a four year period, hubbsi has been found to be much more numerous by subsequent investigators (McLane, 1955). Along the sandy east shore of Lake Eustis, hubbsi is very common. Collections the size of that made by Carr may be obtained in a few seine hauls. Along the east shore of Lake Harris on 14 April 1973, I collected 30 specimens in one seine haul and a total of 94 in six hauls. Suitable habitat may be quite extensive when considering an area one to two feet wide along much of the shore of these large lakes. Although the ecological condition of these lakes has declined radically in recent years (Brezonik et al., 1969), no decline in the abundance of hubbsi is evident. If any change has occurred, it has been an increase in abundance over levels reported by Carr (1936a), Reid (1949), Hellman (1953), and McLane (1955).

Habitat. Populations of hubbsi inhabit a narrow ecological zone which is limited to 1-2 feet of shore line (McLane, 1955). In Lake

Weir, I found individuals swimming in 1-3 inches of water along the shore where moderate wave action is present. In all of the lakes where hubbsi is known to occur, areas exist where wave action has created extensive sandy beaches with moderate stands of Panicum. This fish seems to be normally restricted to these wave-washed areas, although a few specimens have been collected in trouls or in block net-rotenone samples at depths from five to fifteen feet (McLane, 1955; Hellman, 1953; personal observations). The quality of the Oklawaha lakes has declined radically in recent years as a result of eutrophication. Chemical and biological characteristics of the major lakes of the basin are shown in Table 33; all are considered to be eutrophic. Lake Weir is in better condition than the other lakes of the basin, but it is bordering between mesotrophy and eutrophy. As seen by the chemical and biological data of Table 33, Lake Dora has the highest degree of chemical enrichment and productivity and thus is in the most advanced state of eutrophy of the lakes inhabited by hubbsi (Brezonik et al., 1969). The lakes of Table 33 are arranged according to relative advancement of eutrophication. Brezonik et al., (1969) stated that a correlation existed in these lakes between high trophic level and high concentrations of major ions. The water chemistry of Lake Weir differs considerably from the other lakes in that alkalinity and hardness are low, the pH is near neutral, and chloride concentrations are high. Specimens of hubbsi were examined from Lake Yale; however, no chemical data on this lake was available.

Size. Carr (1936a) reported that hubbsi was a small form, with adult males ranging in size from 20-27 mm SL and females 23-31 mm SL. McLane (1955) noted that the largest hubbsi collected were

females from 21-25 mm SL. Subsequently, larger specimens have been collected by Christensen (1965) and myself. As seen in Table 40, the largest specimens examined in this study were a male 40.2 mm SL and a female 36.3 mm SL. The largest female obtained (41.1 mm SL) was not used because of the poor condition of the specimen. Specimens larger than those reported by Carr (1936a) and McLane (1955) seem to be relatively abundant in the Oklawaha lakes; generally, however, hubbsi does not reach the size of variegatus.

Pigmentation. This form has considerable ability to change pigmentation shading depending on the nature of its habitat. Pigmentation is generally reduced in most preserved hubbsi specimens since they are taken from areas of lakes with clean, white sandy bottoms. When specimens are placed in a dark-colored environment such as a dark aquarium, pigmentation gradually becomes darker. I can detect no consistent difference in pigmentation which would distinguish hubbsi from other Cyprinodon populations in Florida.

Feeding Habits. Populations of hubbsi seem to have a diet consisting of animal matter. McLane (1955) noted that the stomachs contained no plant material or sand. Food was found to consist primarily of crustaceans and insect larvae which were not masticated. Specimens of variegatus from the St. Johns River, by contrast, had stomachs containing primarily macerated vegetable matter. Thus McLane (1955) postulated on the divergence of the food habits of these two forms. The carnivorous habit of hubbsi might be under seasonal influence since Harrington and Harrington (1961) found that during periods of high concentrations of mosquito larva, salt

marsh variegatus converted to almost entirely carnivorous feeding. Martin (1970) noted that variegatus from the Texas coast ingested plant materials only accidently while foraging for animal food. The food habits of hubbsi merit additional study.

Character Diagnosis. As already noted, the morphometric characters used by Carr (1936a) to describe hubbsi are correlated with environmental factors. A reduction in depth measurements has been demonstrated among freshwater Cyprinodon populations as well as in hubbsi from less eutrophic lakes. Thus a number of factors are contributing to character differentiation in Florida Cyprinodon populations. These factors include genetics, period of isolation, geographical range, salinity of habitat, and productivity of the habitat.

Among Florida Cyprinodon populations, hubbsi demonstrates extreme values for a number of characters. Circumference scale counts (Figure 3, Table 6), body depth (Figures 5 and 6, Table 14), caudal peduncle depth (Figure 8, Table 16), predorsal length (Figure 9, Table 17), pectoral origin to dorsal origin (Table 21), head length (Figure 14, Table 23), head depth (Figures 15 and 16, Table 24), interorbital width (Figure 18, Table 28), and except for one or two other populations, body width (Figure 7, Table 15), prepectoral length (Table 19), postorbital head length (Figure 17, Table 27), and orbit to angle of preopercle (Figure 20, Table 30) all show hubbsi to possess extreme low values. Extreme high values are found in anal origin to caudal base length (Figures 11 and 12, Table 20) and lateral scale counts (Figure 2, Table 4). These characters

with the exceptions of lateral scales, predorsal length, anal origin to caudal base, and orbit to angle of preopercle seem to be correlated with salinity since all freshwater populations tend to have values diverging in the same direction. Genetic adaptation which parallels that of the environment and which is dependent on period of isolation may be indicated. Thus among freshwater Florida Cyprinodon, hubbsi is more extreme because of its longer period of isolation. It is possible that only time separates hubbsi from other freshwater populations.

Apparent genetic differentiation achieved by hubbsi may be a result of decreased efficiency of food conversion in their freshwater habitat (Kinne, 1966). This is supported by an increase in depth measurements and other characters among lakes with increased eutrophication and production. The extreme character values demonstrated by hubbsi are then a consequence of the increased period of time for genetic adaptations to a freshwater habitat and strictly environmentally induced changes.

The four characters for which hubbsi is nearly extreme and little or no salinity relationship is indicated demonstrate the existence of limited genetic differentiation. High values are shown by lateral scales and anal origin to caudal base while predorsal length and orbit to angle of preopercle have low values. A continuous cline south along the west coast and north along the east coast is suggested for some of these characters. Values for hubbsi are closest to those for Cyprinodon populations from the northwest Florida coast.

For purposes of identification of hubbsi, the combination of characters of anal origin to caudal base divided by body depth may

be used. Results of these calculations are shown for females in Figure 22 and males in Figure 23. This combination of characters was used since anal origin to caudal base was found to be high with no effect induced by salinity and body depth showed extreme low values, although it is recognized that an environmental correlation is indicated. Values greater than 1.0 are usually found for hubbsi (anal origin to caudal base greater than body depth). Differentiation from other Florida Cyprinodon is greater in the males in this respect. Anal origin to caudal base was found by analysis of covariance to have equal means among the various lake populations of male hubbsi studied. A low correlation coefficient ($r = 0.178$) between anal origin to caudal base and body depth also demonstrates the value of these characters.

Origin and Extent of Differentiation. Geological information on the recent drainage relationships of the Oklawaha River and its headwaters has already been discussed. The lakes inhabited by hubbsi were formed as depressions in the bottom of the Penholoway Sea during the Late Pliocene or Early Pleistocene (Cooke, 1939 and Alt and Brooks, 1965). By the Aftonian glaciation and subsequent formation of the Talbot terrace (Alt and Brooks, 1965), the lakes at the headwaters were probably essentially isolated from the estuary which existed in what is now the Oklawaha River Basin, although some drainage from these lakes may have been present. According to White (1958) the Oklawaha River was formed after the headwater lakes and drained a lagoon behind adjacent beach ridges. Thus the drainage was determined by the lakes (White, 1972).

FIGURE 22

Anal origin to caudal base divided by body depth for females of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

ANAL ORIGIN TO CAUDAL BASE

DIVIDED BY BODY DEPTH

FEMALES

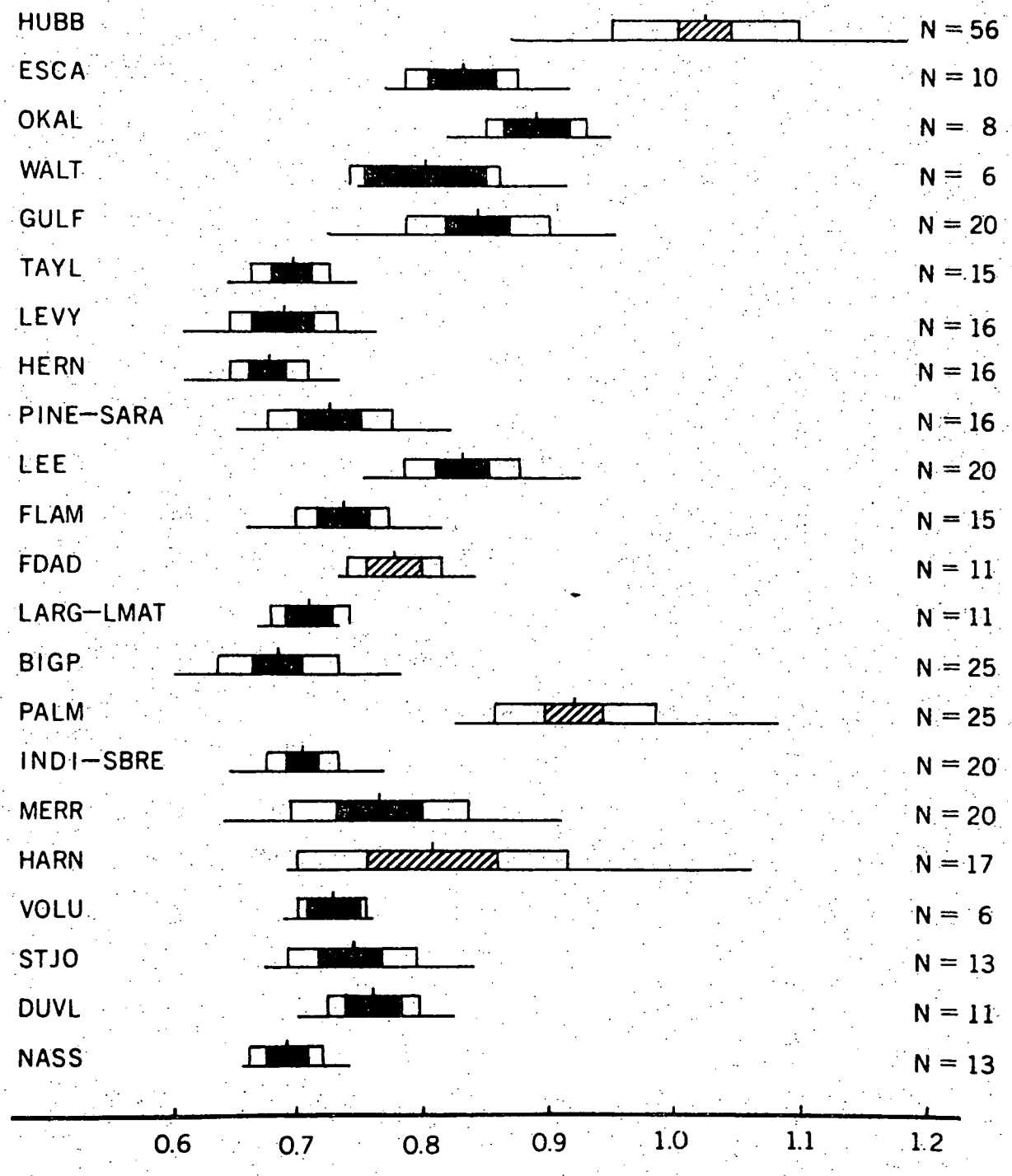


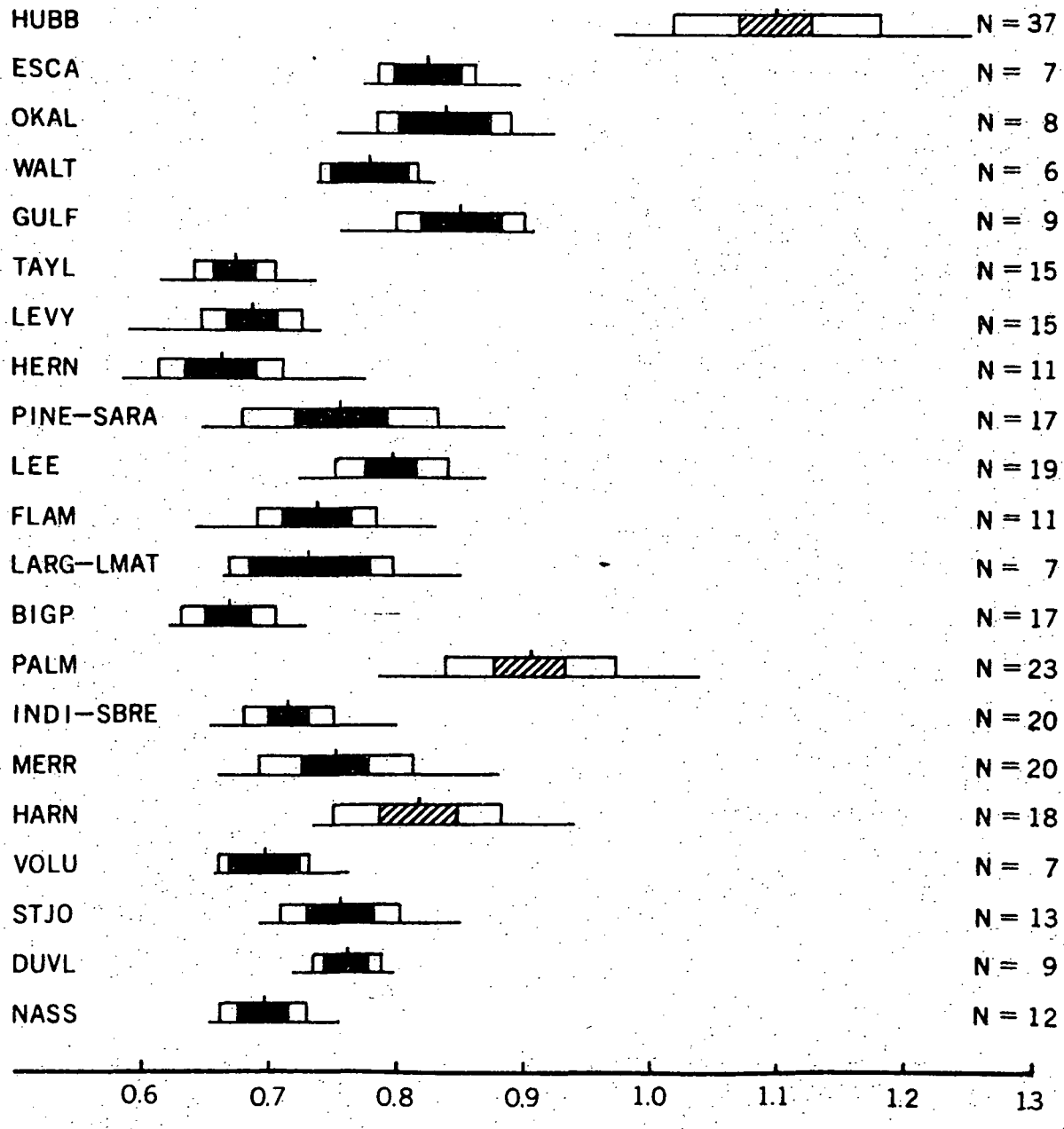
FIGURE 23

Anal origin to caudal base divided by body depth for males of Florida Cyprinodon populations. Vertical line = mean; horizontal line = range; black (brackish or coastal populations) or diagonal lined (freshwater populations) rectangle = two standard errors on either side of mean; white rectangle plus black or diagonal lined rectangle = one standard deviation on either side of mean. Descriptions of four-letter codes for populations are given in Materials Examined.

ANAL ORIGIN TO CAUDAL BASE

DIVIDED BY BODY DEPTH

MALES



With the formation of the Talbot terrace, any possible capture of the headwaters of the Oklawaha River by the Withlacoochee was probably cut off at the Lake Harris Cross Valley. During this period the Withlacoochee River was captured by the Hillsborough River (White, 1958, 1972). This estuary was probably a much more direct route to the sea than was that of the Oklawaha and St. Johns River.

When the sea dropped to the 25 foot level during the Yarmouth interglaciation and formed the Pamlico terrace, isolation of Oklawaha headwaters was essentially complete. The extent of any drainage associated with these lakes during the Pamlico Sea is unknown.

Geological data suggests that hubbsi may have been isolated as early as the Aftonian glaciation but probably at least by the Yarmouth. However, the unknown status of drainage connections during these periods and the ability of Cyprinodon to penetrate freshwater rivers makes it difficult to date geological isolation of this fish.

Death Valley Cyprinodon have undergone extensive speciation since the Wisconsin glaciation. C. salinus, milleri, and nevadensis existed in an area where there was a continuous river only 4000 years ago (Miller, 1948, 1950). Subspecies of nevadensis have evolved in as little as a few hundred years (LaBounty, 1972). Miller (1950) stated that reduced population sizes, extreme environmental conditions of high salinities and temperatures, and increased number of generations per year are conditions which have contributed to the high speciation rate in these pupfish.

There is no geological evidence to suggest that the drainages of the Oklawaha and its headwaters were any different during the Wisconsin

than they are today. No change is evident from areas around the Silver Bluff terrace which was formed during the Sangamon. There is no doubt that hubbsi has been isolated since the Wisconsin, but the abnormal environmental conditions characteristic of the desert pupfish habitats do not exist at the headwaters of the Oklawaha.

Limited differentiation has occurred in hubbsi, but these genetic adaptations mostly parallel those of environmental influences. Those characters for which hubbsi may be genetically extreme are mostly obscured by environmental effects. Some strictly genetic adaptations are suggested for predorsal length, anal origin to caudal base, and orbit to angle of preopercle; however, differentiation of these characters is minor.

Characters previously discussed for which hubbsi is extreme and which show little environmental influence indicate that its closest relationship is with Cyprinodon from the northwest Florida coast. Populations of hubbsi probably were derived through the Lake Harris Cross Valley and Withlacoochee to Hillsborough Rivers. Other characters also suggest a west coast relationship. No relationship with the east coast, through the St. Johns River, is suggested.

Because of the environmental influence on most distinguishing characters, lack of significant genetic differentiation of any other characters, and lack of any extreme environmental factors, I cannot support the present species status of hubbsi. However, because hubbsi is the only Florida Cyprinodon inhabiting waters above the Pamlico terrace, and because of its period of isolation, limited differentiation, and unusual habitat, recognition as a subspecies of C. variegatus is suggested.

South Florida Race

The existence of a distinct south Florida race is revealed by several counts and measurements. Scale counts of belly to dorsal origin (Table 7), dorsal origin to anal origin (Table 8), dorsal origin to pelvic origin (Table 9), belly scales (Figure 4, Table 10), circumference scales (Figure 3, Table 6) and possibly predorsal scales (Table 5) show the same pattern of variation. Character values increase clinally southward along both the east and west coasts. The increase generally proceeds through Sarasota County on the west and Indian River County on the east. Populations, both fresh and coastal, south of these areas demonstrate an abrupt reduction in the number of scales for these characters. This type of trend is also suggested by pelvic fin length (Figure 13) and head length (Figure 14), although there is more irregular scatter in the data. The increasing southward trend along the coasts suggests a temperature influence on coastal variegatus not demonstrated among this south Florida group. Caudal fin rays (Table 3) are generally low in south Florida but do not show clear north-south trends.

Low suborbital scale counts (Table 11) are characteristic of populations at Big Pine and Lower Matecumbe Keys. Lateral and belly scale counts (Figures 2 and 4) exhibit their lowest values in the Keys and in south Florida at Flamingo. All other meristic characters indicated above demonstrate low values in the Keys and generally low values throughout brackish and fresh waters of south Florida, although differences are less discrete in areas more distant from the Keys. This suggests that the south Florida race originated in

the Keys and exists there in its purest form. This race (or its genes) has spread northward into south Florida, its distinctive traits persisting in varying degrees due to different selective pressures or introgression with peninsular populations.

Geological data also support such a hypothesis. All south Florida Cyprinodon populations which exist in fresh water and which I include in the south Florida race exist on the Pamlico terrace. Thus no population could have been established until the water level dropped following the Yarmouth interglaciation (Alt and Brooks, 1965).

As previously indicated, the Florida Keys were also formed during the Pamlico time. The southern Keys were formed first and were connected across Florida Bay with the southwest tip of the peninsula. The southern Keys were then isolated when Florida Bay submerged (Duellman and Swartz, 1958; White, 1972). During the later formation of the upper Keys, any variegatus in the southern Keys would have had an opportunity to move northward and populate the recently emerged southern tip of the peninsula. If Big Pine and the other southern Keys were inhabited by a distinct population, range expansion and/or gene flow could have proceeded northward via this avenue.

It is possible that the variegatus found along the east and west Florida coasts may have been continually distributed around the tip of the peninsula during Pamlico times. During the Yarmouth interglaciation, the southern end of the peninsula terminated north of Lake Okeechobee, about the point where clinal increases in scale counts along the east

and west coasts abruptly stop. When the water level fell, these populations were separated by the rising of what is now southern Florida and were replaced by or interbred with a race spreading northward from the Florida Keys.

The distribution of the proposed south Florida race extends from the Keys northward through the southern tip of the peninsula. I arbitrarily set the northern limit as a line between Fort Myers, Lake Okeechobee, and West Palm Beach. All freshwater populations on the Pamlico terrace are included. It is recognized that some included populations, especially toward the north, show varying degrees of intergradation.

Some question as to the inclusion of southern freshwater populations into this south Florida race are raised by generally reduced circumference scale counts in freshwater areas. It is possible that these freshwater populations have low scale counts as a result of environmental influence rather than genetic similarity to other southern populations. I feel, however, that environmental influences are not great enough to cause scale counts to differ drastically from those of adjacent coastal populations.

Several authors have associated the Florida Keys' populations with the name riverendi (Jordan and Evermann, 1896; Fowler, 1906; Breder, 1932; Hubbs, 1936). All have suggested that riverendi has fewer lateral scales than variegatus. Hubbs (1936), however, reported low scale counts for riverendi from Kingston, Jamaica, but not from Florida Keys' samples that he referred to by the same name. Data presented herein show that the south Florida race does have

lower scale counts than other Florida populations. However, I hesitate to suggest that this race originated from a riverendi stock in the Keys until a thorough analysis clarifies the status of Caribbean Cyprinodon populations.

SUMMARY

1. The distribution of Florida populations of Cyprinodon variegatus variegatus encompasses brackish coastal lagoons and estuaries and the more-saline freshwaters of the Pamlico terrace. Cyprinodon variegatus hubbsi is limited in distribution to the major lakes at the headwaters of the Oklawaha River.

2. Despite euryhaline and eurythermal abilities and the apparent lack of other intrinsic limiting factors, C. v. variegatus is essentially restricted to the more saline waters in its "fresh water" range. Its distribution is probably limited by a combination of factors.

3. Sexual dimorphism is marked, particularly in the following measurements: body depth, body width, caudal peduncle depth, predorsal length, dorsal origin to caudal base, anal origin to caudal base, pectoral origin to dorsal origin, pelvic length, head depth, cheek height, interorbital bony width, orbit length, and orbit to angle of preopercle. For all characters examined, the mean value of the males was greater in every case except body width and predorsal length. No sexual dimorphism is present in any meristic characters studied.

4. The range of morphological variation and trends in geographical variation are described for Florida Cyprinodon variegatus populations.

5. Changes in morphological characters correlated with variations in salinity and temperature are evident within Florida populations of Cyprinodon variegatus. All depth measurements, as well as many other characters, are less at reduced salinity. Trends which may be correlated with salinity all appear to have lower means in freshwater populations. The absence of converse trends may indicate that efficiency of growth and thus body proportions are reduced in Cyprinodon populations inhabiting fresh water. Observed differences are probably due to genetic adaptions that parallel those caused by the environment.

6. Because of the environmental influence on most distinguishing characters and lack of significant genetic differentiation of any other characters, hubbsi is not recognized at the specific level. However, because it is the only Florida Cyprinodon race inhabiting fresh waters above the Pamlico terrace, and because of its period of isolation, limited differentiation, and unusual habitat, recognition as a subspecies of C. variegatus is suggested.

7. Lake populations of C. v. hubbsi show an increase in all depth measurements, circumference scale counts, and other characters, correlated with increasing lake productivity. This may be a result of decreased efficiency of food conversion and physiological stress in their freshwater habitat.

8. A distinct race of C. v. variegatus from the southern tip of the Florida peninsula is characterized by low values for most scale counts and by differentiation in a few morphometric characters. This race may have originated in the Florida Keys and now exists there in its purest form.

9. The geologic and hydrologic history of Florida are discussed as they relate to the past and present distribution of this species.

APPENDIX

Description of four-letter codes for populations are given in Materials Examined.

TABLE 1. Frequency Distribution of Dorsal Rays in Florida Cyprinodon.

Location or Population	9	10	11	12	13	N	$\bar{X}$	S.E.
HUBB*	1	16	49	11		77	10.91	.07
ESCA		3	9	3		15	11.00	.17
OKAL		5	9			14	10.64	.13
WALT		3	8	1		12	10.83	.17
GULF		1	15	4		20	11.15	.11
TAYL			6	11	3	20	11.85	.15
LEVY		1	11	6		18	11.28	.14
HERN			6	12	2	20	11.80	.14
PINE			18			18	11.00	.00
SARA		5	10			15	10.67	.13
LEE		11	8	1		20	10.50	.14
ALVA*		1	9			10	10.90	.10
FLAM		4	12			16	10.75	.11
FDAD*			8	1		9	11.11	.11
LARG		1	5	1		7	11.00	.22
LMAT		6	3			9	10.33	.17
BIGP		16	19	2		37	10.62	.10
PALM*		10	24	2		36	10.78	.09
OKEE*		4	3			7	10.43	.20
INDI		1	2	2		5	11.20	.37
SBRE		3	12	4		19	11.05	.14
MERR*		5	25	4		34	10.97	.09
HARN		8	15	3	1	27	10.89	.14
VOLU		3	10	2		15	10.93	.15
STJO			12	7	1	20	11.45	.13
DUVL		5	14	1		20	10.80	.12
NASS		4	15	1		20	10.85	.11

*Fresh water populations.

TABLE 2. Frequency Distribution of Anal Rays in Florida Cyprinodon.

Location or Population	9	10	11	12	N	$\bar{X}$	S.E.
HUBB*	10	63	5		78	9.93	.05
ESCA		14	1		15	10.07	.07
OKAL	1	12	1		14	10.00	.10
WALT		11	1		12	10.08	.08
GULF	1	13	6		20	10.25	.12
TAYL		11	8	1	20	10.50	.13
LEVY		9	9		18	10.50	.12
HERN		12	8		20	10.40	.11
PINE		15	3		18	10.17	.09
SARA	1	12	2		15	10.07	.12
LEE	1	19			20	9.95	.05
ALVA*		6	3		9	10.33	.17
FLAM		15	1		16	10.06	.06
FDAD*		9			9	10.00	.00
LARG		7			7	10.00	.00
LMAT	1	8			9	9.89	.11
BIGP	1	31	4		36	10.08	.06
PALM*	2	31	3		36	10.03	.06
OKEE*		7			7	10.00	.00
INDI		5			5	10.00	.00
SBRE		19			19	10.00	.00
MERR	2	29	3		34	10.03	.07
HARN*		19	8		27	10.29	.09
VOLU		13	2		15	10.13	.09
STJO	1	18	1		20	10.00	.07
DUVL	2	14	4		20	10.10	.12
NASS	2	15	3		20	10.05	.11

*Fresh water populations.

TABLE 3. Frequency Distribution of Caudal Rays in Florida Cyprinodon.

Location or Population	13	14	15	16	17	18	N	$\bar{X}$	S.E.
HUBB*	1	33	28	14	2		78	14.78	.10
ESCA	1	7	5	2			15	14.53	.21
OKAL		6	6	2			14	14.71	.19
WALT		3	4	5			12	15.17	.24
GULF		8	9	3			20	14.75	.16
TAYL			1	19			20	15.95	.05
LEVY		3	3	11			17	15.47	.19
HERN		7	5	8			20	15.05	.20
PINE		5	5	7	1		18	15.22	.22
SARA			6	7			13	15.54	.14
LEE	1	12	5	2			20	14.40	.17
ALVA*		6	4				10	14.40	.16
FLAM		11	1	3			15	14.47	.21
FDAD*		7		2			9	14.44	.29
LARG		4	1	2			7	14.71	.36
LMAT	1	4	1				6	14.00	.26
BIGP		21	8	6			35	14.57	.13
PALM*		10	10	15	1		36	15.19	.15
OKEE*	1	5					6	13.83	.17
INDI			3	1			4	15.20	.25
SBRE		1	8	10			19	15.47	.14
MERR		15	8	11			34	14.88	.15
HARN*	1	14	5	7			27	14.67	.18
VOLU		6	6	3			15	14.80	.20
STJO	1	5	8	6			20	14.95	.20
DUVL		1	5	11	3		20	15.80	.17
NASS		2	9	7	1	1	20	15.50	.21

*Fresh water populations.

TABLE 4. Frequency Distribution of Lateral Scales in Florida Cyprinodon.

Location or Population	22	23	24	25	26	27	N	$\bar{X}$	S.E.
HUBB*			28	52	11	1	92	24.84	.07
ESCA				12	3		15	25.20	.11
OKAL			7	7			14	24.50	.14
WALT			2	10			12	24.83	.11
GULF			11	9			20	24.45	.11
TAYL				18	2		20	25.10	.07
LEVY		1	12	5			18	24.22	.13
HERN			10	10			20	24.50	.11
PINE		3	7	8			18	24.28	.18
SARA		1	13	1			15	24.00	.10
LEE		3	15	2			20	23.95	.11
ALVA*		1	8	1			10	24.00	.15
FLAM	1	14	1				16	23.00	.09
FDAD*			7	2			9	24.22	.15
LARG	1	4	2				7	23.14	.26
LMAT	4	5					9	22.55	.17
BIGP	11	23	3				37	22.78	.10
PALM*		1	18	17			36	24.44	.09
OKEE*			4	3			7	24.43	.20
INDI		1	3	1			5	24.00	.32
SBRE	1	2	16				19	23.79	.12
MERR	1	4	23	6			34	24.00	.11
HARN*		2	22	3			27	24.04	.08
VOLU		2	12				14	23.86	.10
STJO		8	11	1			20	23.65	.13
DUVL		1	16	3			20	24.10	.10
NASS		6	13	1			20	23.75	.12

*Fresh water populations.

TABLE 5. Frequency Distribution of Predorsal Scales in Florida Cyprinodon.

Location or Population	8	9	10	11	12	13	N	$\bar{X}$	S.E.
HUBB*		7	81	5			93	9.98	.04
ESCA		1	8	6			15	10.33	.16
OKAL		1	9	4			14	10.21	.15
WALT			6	6			12	10.50	.15
GULF		3	11	6			20	10.15	.15
TAYL			6	12	1	1	20	10.85	.17
LEVY		1	13	4			18	10.17	.12
HERN		1	11	7	1		20	10.40	.15
PINE		3	7	7	1		18	10.33	.20
SARA		1	9	5			15	10.27	.15
LEE		4	14	2			20	9.90	.12
ALVA*		1	9				10	9.90	.10
FLAM		2	13	1			16	9.94	.11
FDAD*			7	2			9	10.22	.15
LARG		2	4	1			7	9.86	.26
LMAT			9				9	10.00	.00
BIGP	1	10	25	1			37	9.70	.09
PALM*			32	4			36	10.11	.05
INDI			4	1			5	10.20	.20
SBRE		2	13	4			19	10.10	.13
MERR			27	6	1		34	10.23	.08
HARN*			10	17			27	10.63	.09
VOLU			10	5			15	10.33	.13
STJO		2	18				20	9.90	.07
DUVL			13	7			20	10.35	.11
NASS			11	9			20	10.45	.11

*Fresh water populations.

TABLE 6. Frequency Distribution of Circumference Scales in Florida Cyprinodon.

Location or Population	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	N	$\bar{X}$	S.E.
HUBB*	8	11	20	10	19	15	4	4	1	1											93	28.24	.21
ESCA						2	2	3	1	4	1	1	1								15	33.00	.54
OKAL				3		1	4	4	2												14	30.86	.47
WALT						3	1	2	3				2		1						12	33.08	.87
GULF						1	2	2	2		2	5	2	2	2						20	35.00	.62
TAYL													3	3	1	2	7	2	1	1	20	40.10	.46
LEVY								3	3	1	3	2	1	3	1			1			18	35.44	.66
HERN						1		2	1	2		1	1	3	3	4	1	1			20	37.10	.77
PINE								1			2	1	2	3	2	2	2	2	1		18	38.50	.68
SARA									1	1	2	1	2	2	2	2	2				15	37.53	.65
LEE					1	1	5	4	2	3	2		1	1							20	32.75	.51
ALVA*						1	3	3	1	2											10	32.00	.42
FLAM								2	3	5	2	3	1								16	34.25	.37
FDAD*				1			1	5		2											9	31.89	.59
LARC					1	2	2		1				1								7	31.57	1.02
LMAT							1	3	2	1	2		1								9	33.33	.64
BIGP				1	1	5	4	7	11	4	1	2	1								37	32.38	.32
PALM*		1	4	1	12	4	7	2	5												36	29.89	.32
OKEE*					1		2	3	1												7	31.43	.48
INDI											1			1	1		2				5	38.80	1.11
SBRE									2		1	3	3	1	3	3	1	1		1	19	38.00	.66
MERR								1	3	7	9	2	6	4	1	1					34	35.56	.33
HARN*			2		1	4	9	3	2		4	1		1							27	31.78	.50
VOLU									2	3	3	2	3		1	1					15	35.67	.53
STJO					1		5	3	2	5	2	1	1								20	32.95	.45
DUVL								3	3	10	3		1								20	33.85	.26
NASS						1	1	7	1	3	5	1				1					20	33.55	.50

*Fresh water populations.

TABLE 7. Frequency Distribution of Dorsal Origin to Belly Mid-line Scales in Florida Cyprinodon.

Location or Population	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{X}$	S.E.
HUBB*	13	36	21	20	1	1						92	15.60	.11
ESCA			1	3	4	6		1				15	18.27	.31
OKAL			4	7	2	1						14	17.00	.23
WALT				7	2	1		2				12	18.00	.44
GULF			1	2	2	5	6	3	1			20	19.30	.34
TAYL						1	2	8	4	5		20	21.50	.26
LEVY				1	3	4	5	2	2	1		18	19.78	.37
HERN			1		3	2	4	3	6	1		20	20.30	.41
PINE				1		2	3	2	5	2	3	18	21.39	.46
SARA						1	2	5	3	3	1	15	21.53	.35
LEE				5	10	2	1	2				20	18.25	.27
ALVA*				3	4	2	1					10	18.10	.31
FLAM					5	7	3		1			16	19.06	.26
FDAD*		1		3	3	2						9	17.55	.41
LARG			1	5			1					7	17.28	.47
LMAT				3	5	1						9	17.78	.22
BIGP	1	1	7	8	15	4	1					37	17.38	.20
PALM*	1	6	9	13	6	1						36	16.55	.19
OKEE*		1		5	1							7	16.86	.34
INDI							1	1	1	2		5	21.80	.58
SBRE					1	2	4	4	2	4	2	19	21.26	.40
MERR				1	3	10	8	6	5			33	19.91	.23
HARN*			3	3	15	3	2		1			27	18.07	.24
VOLU				1	2	3	4	2	3			15	19.87	.40
STJO			2	7	9	1		1				20	17.65	.24
DUVL					6	8	4	2				20	19.10	.22
NASS				2	7	6	2	3				20	18.85	.27

*Fresh water populations.

TABLE 8. Frequency Distribution of Dorsal Origin to Anal Origin Scales in Florida Cyprinodon.

Location or Population	11	12	13	14	15	16	17	18	N	$\bar{X}$	S.E.
HUBB*	7	60	25	1					93	12.21	.06
ESCA		4	9	2					15	12.87	.16
OKAL			10	4					14	13.28	.12
WALT		1	4	4	3				12	13.75	.28
GULF			3	7	9		1		20	14.45	.21
TAYL				1	4	10	5		20	15.95	.18
LEVY				3	7	7		1	18	15.39	.23
HERN			2	2	3	6	6	1	20	15.75	.31
PINE				2	2	9	5		18	15.94	.22
SARA				1	1	7	5		14	16.14	.23
LEE		2	10	8					20	13.30	.15
ALVA*	1	2	5	1	1				10	12.90	.35
FLAM			6	9	1				16	13.69	.15
FDAD*		1	6	2					9	13.11	.20
LARG		1	5	1					7	13.00	.22
LMAT			5	3	1				9	13.56	.24
BIGP		1	19	11	5	1			37	13.62	.14
PALM*		8	18	10					36	13.05	.12
INDI				2	1	2			5	15.00	.45
SBRE				2	8	8	1		19	15.42	.18
MERR		2	13	14	4	1			34	13.68	.15
HARN*	2	11	13	1					27	12.48	.13
VOLU			1	9	5				15	14.27	.15
STJO	1	2	10	6	1				20	13.20	.20
DUVL		2	15	3					20	13.05	.11
NASS		1	13	5	1				20	13.30	.15

*Fresh water populations.

TABLE 9. Frequency Distribution of Dorsal Origin to Pelvic Origin Scales in Florida Cyprinodon.

Location or Population	10	11	12	13	14	15	16	17	18	N	$\bar{X}$	S.E.
HUBB*	3	24	48	17	1					93	11.88	.08
ESCA				7	5	3				15	13.73	.21
OKAL			2	7	5					14	13.21	.19
WALT				3	5	2	2			12	14.25	.30
GULF				4	10	4	1	1		20	14.25	.23
TAYL							12	7	1	20	16.45	.13
LEVY				1	5	6	1	5		18	15.22	.31
HERN				2	3	1	6	8		20	15.75	.31
PINE					4	2	9		3	18	15.78	.31
SARA					4	9	2			15	14.87	.16
LEE				7	11	2				20	13.75	.14
ALVA*				4	6					10	13.60	.16
FLAM				3	6	7				16	14.25	.19
FDAD*			2	4	3					9	13.11	.26
LARG			1	4	1	1				7	13.28	.36
LMAT			1	4	4					9	13.33	.23
BIGP			2	13	15	6	1			37	13.76	.15
PALM*		3	10	20	2	1				36	12.67	.14
OKEE*				6	1					7	13.14	.14
INDI					1		1	3		5	16.20	.58
SBRE				1	2	8	5	3		19	15.37	.24
MERR				4	16	11	3			34	14.38	.14
HARN*			6	8	7	4	2			27	13.55	.23
VOLU				2	4	6	3			15	14.67	.25
STJO				5	13	2				20	13.85	.13
DUVL				5	11	3	1			20	14.00	.18
NASS				4	9	5	2			20	14.25	.20

*Fresh water populations.

TABLE 10. Frequency Distribution of Belly Scales in Florida Cyprinodon.

Location or Population	14	15	16	17	18	19	20	21	22	23	24	25	26	27	29	N	$\bar{X}$	S.E.
HUBB*	1	3	14	20	22	11	12	3	4	2			1			93	18.18	.21
ESCA				1	3	3	5	2		1						15	19.53	.39
OKAL			2	1	1	5	4	1								14	18.78	.41
WALT					3	3	1	2	2		1					12	20.08	.56
GULF				1	1	4	5	4	1	2	1	1				20	20.60	.45
TAYL						1		3	3	6	6	1				20	22.75	.32
LEVY			1	2	3	4	1	6	1							18	19.33	.41
HERN					2	2	3	4	5	4						20	21.00	.36
PINE					1	2	3	2	2	2		4		1	1	18	22.44	.71
SARA					1		2	2	2	3	3	1		1		15	22.47	.58
LEE				4	2	8	4	1	1							20	18.95	.30
ALVA*				1	1	1		3								6	19.50	.72
FLAM				1	2	5	5	1	2							16	19.56	.34
FDAD*				1		2	4	1	1							9	19.78	.46
LARG				1	3		2									6	18.50	.50
LMAT			1	4	1	3										9	17.67	.37
BIGP	2	3	9	9	7	3	3									36	17.03	.26
PALM*				3	9	10	11	3								36	19.05	.19
OKEE*				1		2	2	2								7	19.57	.53
INDI								1	2	1	1					5	22.40	.51
SBRE						1	3	3	3	4	4		1			19	22.21	.41
MERR					5	2	9	7	7	3	1					34	20.65	.28
HARN*			1		3	1	11	6	2	1	1	1				27	20.41	.35
VOLU						3	4	3	3	1			1			15	21.00	.48
STJO			1	1	4	8	3	2	1							20	19.05	.31
DUVL		2		2	3	7	3	1	1	1						20	18.85	.44
NASS				1	4	9	2	2	1	1						20	19.35	.33

*Fresh water populations.

TABLE 11. Frequency Distribution of Suborbital Scales in Florida Cyprinodon.

Location or Population	4	5	6	7	8	9	10	N	$\bar{X}$	S.E.
HUBB*		1	2	25	31	16	3	78	7.87	.11
ESCA			2	9	2	2		15	7.27	.23
OKAL				7	4	1		12	7.50	.19
WALT			1	4	4	3		12	7.75	.28
GULF			1	10	7	1	1	20	7.55	.20
TAYL				6	8	5	1	20	8.05	.20
LEVY			4	6	5	3		18	7.39	.24
HERN			1	4	8	6	1	20	8.10	.22
PINE				10	6			16	7.37	.12
SARA				9	3	2		14	7.50	.20
LEE			1	7	10	2		20	7.65	.17
ALVA*				6	3	1		10	7.50	.22
FLAM				8	6	2		16	7.62	.18
FDAD*				5	3	1		9	7.55	.24
LARG				3	3	1		7	7.71	.28
LMAT		3	2	4				9	6.11	.31
BIGP	1	1	9	22	3			36	6.69	.13
PALM*				8	20	8		36	8.00	.11
INDI				2	1	2		5	8.00	.45
SBRE				5	12	2		19	7.84	.14
MERR			2	14	14	4		34	7.59	.13
HARN*			3	12	12			27	7.33	.13
VOLU			1	10	4			15	7.20	.14
STJO			3	12	4	1		20	7.15	.17
DUVL			3	14	2	1		20	7.05	.15
NASS			2	15	3			20	7.05	.11

*Fresh water populations.

TABLE 12. Frequency Distribution of Frontal Scales in Florida Cyprinodon.

Location or Population	3.0	4.0	4.5	5.0	5.5	6.0	N
HUBB*		1	6	79	1	3	90
ESCA				12		3	15
OKAL				12		2	14
WALT			1	10			11
GULF		2	1	16			19
TAYL		1	3	15		1	20
LEVY			5	13			18
HERN			2	18			20
PINE			3	15			18
SARA				10		1	11
LEE		2	3	15			20
ALVA*		1	1	8			10
FLAM		1	1	14			16
FDAD*				9			9
LARG			1	4	1	1	7
LMAT				9			9
BIGP		6	3	27	1		37
PALM*				23	8	5	36
INDI			3	2			5
SBRE		1	4	14			19
MERR		3	13	18			34
HARN*			9	18			27
VOLU		5	5	4			14
STJO		5	9	6			20
DUVL	1	15	3	1			20
NASS		7	7	6			20

*Fresh water populations.

TABLE 13. Standard Length in Millimeters for Cyprinodon from Florida.

Population or Location	Standard Length					
	Males			Females		
	$\bar{X}$	Range	N	$\bar{X}$	Range	N
HUBB*	30.7	26.6-40.2	37	30.7	26.9-36.3	56
ESCA	35.0	28.0-40.7	7	36.2	30.7-43.9	10
OKAL	39.0	31.0-41.5	8	34.1	29.9-44.7	8
WALT	33.4	31.0-35.4	6	35.7	30.5-39.6	6
GULF	35.8	33.6-40.1	9	34.3	28.7-41.0	20
TAYL	36.1	32.4-38.9	15	34.2	30.6-38.8	15
LEVY	36.9	29.2-40.3	15	37.5	31.3-40.4	16
HERN	33.3	30.5-36.1	11	33.9	31.3-36.9	16
PINE-SARA	35.8	30.0-40.8	20	35.2	29.4-40.0	17
LEE	36.1	33.5-38.6	19	36.2	31.8-39.3	20
FLAM	33.7	26.8-37.5	11	32.4	26.9-39.8	15
FDAD*		—		29.1	26.7-32.4	11
LARG-LMAT	30.8	27.8-35.7	7	28.7	26.6-32.2	11
BIGP	31.0	27.0-34.7	17	32.1	29.3-36.4	25
PALM*	33.5	30.4-36.6	23	34.3	31.2-36.9	25
INDI-SBRE	32.2	30.0-34.3	21	33.8	31.0-38.6	20
MERR	35.7	31.9-39.6	20	34.9	30.6-39.3	20
HARN*	36.5	30.6-41.0	18	33.1	31.3-36.2	17
VOLU	39.4	37.1-41.5	7	39.4	34.6-41.7	6
STJO	35.6	30.1-40.1	13	34.8	29.3-37.4	13
DUVL	36.0	31.8-40.1	9	35.2	31.9-40.8	11
NASS	37.4	34.3-40.7	13	37.2	35.1-39.7	13

*Fresh water populations.

TABLE 14. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Body Depth

Population or Location	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	350	4.0	308-396	37	344	3.5	301-409	56
ESCA	434	8.1	394-459	7	420	4.6	396-439	10
OKAL	435	6.8	397-462	8	387	5.5	363-409	8
WALT	447	9.6	410-471	6	431	6.5	403-448	6
GULF	443	6.6	415-481	9	427	3.8	400-471	20
TAYL	494	4.3	467-523	15	478	4.5	446-508	15
LEVY	516	5.7	485-568	15	494	6.0	458-540	16
HERN	522	9.1	460-570	11	496	4.3	464-519	16
PINE-SARA	470	10.9	400-535	17	466	5.7	434-514	16
LEE	441	4.7	415-481	19	413	4.1	376-440	20
FLAM	482	6.3	433-511	11	452	5.3	421-506	15
FDAD*					400	6.1	375-433	11
LARG-LMAT	460	8.0	416-479	7	439	5.9	404-472	11
BIGP	501	3.3	467-521	17	483	4.3	440-525	25
PALM*	394	4.9	358-433	23	369	4.0	325-404	25
INDI-SBRE	496	3.1	463-515	20	474	3.5	451-523	20
MERR	486	9.0	416-571	20	438	6.6	380-488	20
HARN*	435	5.4	390-466	18	386	8.5	311-436	17
VOLU	487	6.6	358-513	7	450	6.8	430-472	6
STJO	499	7.2	448-539	13	453	6.7	396-500	13
DUVL	467	6.3	439-494	9	443	3.4	429-465	11
NASS	501	7.3	466-558	12	475	5.7	437-503	13

*Fresh water populations.

TABLE 15. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Body Width							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	199	2.1	176-230	37	222	2.3	187-252	56
ESCA	238	3.8	221-254	7	250	5.1	223-276	10
OKAL	234	5.2	212-256	8	240	4.4	216-254	8
WALT	254	7.3	220-271	6	261	7.7	233-284	6
GULF	229	3.8	218-252	9	236	2.6	216-265	20
TAYL	263	4.4	226-290	15	255	2.9	231-276	15
LEVY	260	2.7	244-278	15	273	2.7	256-291	16
HERN	248	3.8	230-269	11	263	2.9	249-289	16
PINE-SARA	246	4.8	211-279	20	256	4.6	224-286	17
LEE	230	3.4	204-263	19	235	3.6	203-268	20
FLAM	238	3.5	224-258	11	249	4.8	221-290	15
FDAD*					251	4.0	231-269	11
LARG-LMAT	237	5.1	221-252	7	253	5.1	232-278	11
BIGP	253	4.4	223-287	17	262	4.4	227-305	25
PALM*	209	2.1	191-225	23	218	2.6	182-238	25
INDI-SBRE	238	2.5	217-261	21	253	2.3	239-273	20
MERR	254	4.1	221-285	20	254	5.6	209-299	20
HARN*	239	4.9	198-270	18	271	7.5	209-316	17
VOLU	255	5.2	241-274	7	260	5.5	243-278	6
STJO	252	3.0	233-269	13	280	5.2	234-305	13
DUVL	255	4.9	227-274	9	277	3.7	260-302	11
NASS	278	5.5	241-306	13	293	4.0	264-311	13

*Fresh water populations.

TABLE 16. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

	Caudal Peduncle Depth							
	Males				Females			
Population or Location	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	182	1.5	161-199	37	170	1.4	149-190	56
ESCA	180	2.4	175-192	7	174	2.1	168-189	10
OKAL	203	2.6	190-210	8	182	3.0	174-199	8
WALT	197	2.8	190-208	6	188	4.7	168-197	6
GULF	203	3.0	189-216	9	198	1.1	190-209	20
TAYL	205	1.8	196-218	15	200	2.0	189-219	15
LEVY	219	2.0	208-233	15	206	1.6	194-216	16
HERN	213	1.9	201-222	11	201	2.0	190-221	16
PINE-SARA	207	2.5	183-226	20	196	2.0	180-209	17
LEE	195	2.0	180-211	19	182	1.7	169-197	20
FLAM	223	3.3	205-240	11	200	1.8	189-216	15
FDAD*					178	2.8	163-194	11
LARG-LMAT	201	4.7	189-224	7	193	2.0	180-202	11
BIGP	218	2.1	200-238	17	205	2.0	183-220	25
PALM*	195	1.8	178-208	23	183	1.4	172-195	25
INDI-SBRE	222	1.4	212-237	21	209	1.3	199-221	20
MERR	217	3.8	188-247	20	197	2.5	176-213	20
HARN*	200	1.4	191-214	18	173	1.7	159-188	17
VOLU	212	2.5	205-222	7	200	3.9	185-212	6
STJO	225	3.3	201-239	13	198	2.0	183-210	13
DUVL	208	2.6	197-219	9	193	1.9	182-203	11
NASS	223	2.4	210-237	13	207	2.9	191-223	13

*Fresh water populations.

TABLE 17. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Predorsal Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	528	2.7	489-555	37	543	2.0	511-570	56
ESCA	539	6.2	505-550	7	553	4.7	536-586	10
OKAL	559	2.8	549-570	8	559	4.0	543-581	8
WALT	563	4.5	545-574	6	571	5.1	555-583	6
GULF	544	3.5	524-554	9	552	4.0	525-606	20
TAYL	578	3.1	561-597	15	570	2.5	549-584	15
LEVY	579	4.5	547-610	15	577	3.4	545-592	16
HERN	577	4.1	557-608	11	588	3.8	571-625	16
PINE-SARA	565	3.3	533-588	20	573	4.0	548-598	17
LEE	553	3.7	527-592	19	551	3.2	514-571	20
FLAM	569	4.8	545-601	11	583	4.0	562-613	15
FDAD*					577	5.3	550-602	11
LARG-LMAT	561	4.3	547-575	7	582	3.0	560-593	11
BIGP	568	2.2	552-585	17	580	3.5	548-614	25
PALM*	556	2.0	538-575	23	564	2.3	541-588	25
INDI-SBRE	572	2.6	547-591	21	584	3.4	544-609	20
MERR	555	3.7	522-589	20	568	3.3	534-595	20
HARN*	564	3.6	534-586	18	588	3.6	567-617	17
VOLU	574	8.5	533-596	7	580	4.7	563-591	6
STJO	565	3.9	544-596	13	580	3.3	563-600	13
DUVL	552	3.6	537-572	9	557	2.1	544-564	11
NASS	578	3.6	552-593	13	591	4.1	559-610	13

*Fresh water populations.

TABLE 18. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Dorsal Origin to Caudal Base							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	537	2.8	505-565	37	517	2.3	489-559	56
ESCA	546	5.2	528-569	7	535	3.2	519-554	10
OKAL	548	5.0	523-569	8	520	4.3	500-535	8
WALT	534	4.1	520-551	6	525	8.9	492-555	6
GULF	552	4.6	531-573	9	535	2.6	513-556	20
TAYL	536	3.8	506-568	15	535	3.8	508-554	15
LEVY	560	3.6	534-582	15	545	2.2	530-559	16
HERN	558	1.9	545-571	11	540	3.8	511-558	16
PINE-SARA	553	4.5	506-590	20	537	3.9	507-565	17
LEE	525	3.5	493-557	19	520	2.7	503-550	20
FLAM	541	4.3	520-563	11	512	4.3	482-537	15
FDAD*					501	5.6	467-531	11
LARG-LMAT	540	8.8	518-585	7	509	4.7	483-534	11
BIGP	546	3.8	519-574	17	529	2.2	506-551	25
PALM*	527	1.8	508-542	23	512	2.9	477-544	25
INDI-SBRE	555	3.0	528-576	21	531	3.0	509-560	20
MERR	557	4.1	525-593	20	532	3.6	506-577	20
HARN*	534	3.6	505-558	18	480	3.7	453-507	17
VOLU	540	5.5	520-558	7	519	5.6	501-534	6
STJO	561	4.6	528-590	13	520	4.5	487-543	13
DUVL	560	6.8	535-596	9	528	3.0	515-539	11
NASS	537	3.4	514-555	13	509	4.0	490-535	13

*Fresh water populations.

TABLE 19. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Prepectoral Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	355	1.7	334-380	37	355	1.7	323-387	56
ESCA	353	3.0	344-365	7	355	3.5	340-374	10
OKAL	385	4.7	368-400	8	382	4.6	356-398	8
WALT	359	5.6	341-377	6	350	6.2	328-373	6
GULF	365	2.0	357-372	9	367	2.8	336-389	20
TAYL	372	2.8	357-398	15	375	2.3	362-389	15
LEVY	392	3.6	367-412	15	393	2.4	375-412	16
HERN	386	2.6	374-398	11	387	3.6	355-415	16
PINE-SARA	376	4.0	351-436	20	379	3.5	352-402	17
LEE	381	2.3	361-408	19	376	2.8	357-405	20
FLAM	398	3.5	381-417	11	395	4.3	372-439	15
FDAD*			--		373	5.2	341-394	10
LARG-LMAT	388	5.8	361-406	7	391	4.3	366-414	11
BIGP	389	3.3	364-411	17	390	2.6	368-415	25
PALM*	382	2.8	355-406	23	378	2.7	360-407	25
INDI-SBRE	395	1.8	373-407	21	395	2.1	377-409	20
MERR	393	3.3	368-421	20	389	3.0	369-412	20
HARN*	362	2.4	343-386	18	367	2.8	351-386	17
VOLU	387	3.4	377-401	7	386	2.6	376-394	6
STJO	384	2.9	372-402	13	380	3.6	363-405	13
DUVL	376	2.5	367-390	9	361	2.6	348-378	11
NASS	391	4.6	360-419	13	388	4.8	358-409	13

*Fresh water populations.

TABLE 20. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Anal Origin to Caudal Base							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	384	1.2	370-397	37	348	1.4	326-368	56
ESCA	359	4.0	351-381	7	346	2.4	336-362	10
OKAL	365	3.8	350-378	8	343	4.6	321-365	8
WALT	349	3.8	334-361	6	343	7.6	315-367	6
GULF	378	4.0	362-396	9	358	3.5	324-380	20
TAYL	335	3.2	310-358	15	331	2.5	316-345	15
LEVY	356	3.8	332-382	15	339	2.2	326-357	16
HERN	346	3.0	335-363	11	335	2.7	308-351	16
PINE-SARA	353	2.6	330-377	20	336	4.5	293-357	17
LEE	354	2.9	332-384	19	341	2.6	322-368	20
FLAM	357	3.0	331-369	11	332	3.2	311-357	15
FDAD*					311	5.6	283-341	11
LARG-LMAT	338	8.0	307-360	7	311	3.4	295-329	11
BIGP	338	3.7	312-366	17	331	3.2	298-368	25
PALM*	358	2.2	334-374	23	339	2.1	313-354	25
INDI-SBRE	359	2.6	337-380	21	334	2.6	311-357	20
MERR	367	3.3	336-393	20	334	3.2	307-363	20
HARN*	357	3.1	340-391	18	308	3.2	293-335	17
VOLU	342	4.5	327-361	7	328	1.2	326-333	6
STJO	380	2.5	359-390	13	336	4.6	309-361	13
DUVL	358	3.6	339-377	9	338	3.1	323-354	11
NASS	351	3.2	333-371	13	328	3.7	304-360	13

*Fresh water populations.

TABLE 21. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Pectoral Origin to Dorsal Origin							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	322	3.8	278-367	37	329	2.4	299-372	56
ESCA	376	9.0	345-413	7	374	4.2	352-396	10
OKAL	378	5.7	348-406	8	353	4.7	333-378	8
WALT	401	6.3	376-419	6	399	6.8	370-412	6
GULF	386	4.0	367-409	9	379	3.8	353-426	20
TAYL	419	3.0	396-435	15	400	3.3	385-429	15
LEVY	427	5.9	395-479	15	409	3.7	388-436	16
HERN	427	7.2	384-474	11	413	2.1	397-423	16
PINE-SARA	413	8.5	353-461	20	405	4.7	363-427	17
LEE	384	3.3	364-416	19	366	3.2	336-392	20
FLAM	413	6.0	362-443	11	394	4.4	370-435	15
FDAD*			--		364	4.9	331-384	10
LARG-LMAT	386	6.4	356-412	7	388	4.4	359-410	11
BIGP	414	3.0	386-441	17	408	3.6	375-442	25
PALM*	342	3.5	316-365	23	337	3.0	300-355	25
INDI-SBRE	420	3.2	390-453	21	414	2.4	397-429	20
MERR	408	7.2	354-473	20	384	5.2	344-434	20
HARN*	401	6.3	353-445	18	376	6.0	317-415	17
VOLU	427	6.0	403-451	7	410	2.5	405-419	6
STJO	419	7.1	365-452	13	406	4.4	373-432	13
DUVL	408	4.8	385-426	9	397	2.8	381-411	11
NASS	434	3.4	411-449	13	422	3.1	409-446	13

*Fresh water populations.

TABLE 22. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Pelvic Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	135	0.9	123-148	37	127	0.9	113-139	55
ESCA	130	2.9	120-142	7	121	1.3	115-127	10
OKAL	137	1.6	132-145	8	125	1.7	120-134	8
WALT	136	1.7	130-142	6	129	2.6	119-135	6
GULF	142	2.6	127-153	9	138	1.3	125-147	20
TAYL	139	2.1	126-152	15	137	1.6	120-146	15
LEVY	152	2.0	141-164	15	141	1.5	134-154	15
HERN	144	2.6	124-158	11	135	2.0	126-152	16
PINE-SARA	151	1.8	137-168	20	142	1.3	133-155	17
LEE	130	1.7	115-149	19	119	1.5	108-133	20
FLAM	148	3.9	125-165	11	133	1.3	124-141	14
FDAD*			--		126	1.3	120-135	11
LARG-LMAT	139	2.3	129-146	7	126	1.4	118-131	11
BIGP	145	1.9	133-163	17	142	1.3	131-156	25
PALM*	130	1.5	118-142	23	122	0.8	116-135	25
INDI-SBRE	160	1.3	147-171	21	151	1.5	135-163	20
MERR	152	2.6	126-170	20	139	2.1	122-155	20
HARN*	131	1.8	118-141	18	120	1.9	102-139	17
VOLU	138	2.8	130-148	7	131	2.1	126-141	6
STJO	153	2.1	141-167	13	144	2.0	131-160	13
DUVL	139	1.5	132-146	9	130	1.5	124-138	11
NASS	146	2.1	133-157	13	138	1.6	127-149	13

*Fresh water populations.

TABLE 23. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Head Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	325	1.4	303-343	37	323	1.3	301-340	56
ESCA	320	3.9	307-336	7	322	3.0	310-336	10
OKAL	337	1.4	333-345	8	330	2.8	320-342	8
WALT	328	3.4	319-342	6	320	4.5	300-331	6
GULF	340	2.4	327-352	9	340	2.9	307-365	20
TAYL	341	2.4	321-355	15	342	2.3	326-359	15
LEVY	348	2.5	338-373	15	349	2.6	328-365	16
HERN	348	2.4	326-356	11	346	2.4	330-364	16
PINE-SARA	341	2.3	326-374	20	344	3.3	320-370	17
LEE	355	2.3	334-383	19	348	2.1	331-364	20
FLAM	364	2.6	349-375	11	363	3.6	347-398	15
FDAD*					334	3.3	315-350	11
LARG-LMAT	342	4.2	330-363	7	344	2.5	332-360	11
BIGP	354	2.3	331-368	17	351	1.8	336-367	25
PALM*	338	1.9	320-351	23	335	1.8	316-349	25
INDI-SBRE	365	1.8	350-384	21	361	2.2	342-378	20
MERR	354	3.6	313-379	20	352	2.8	334-386	20
HARN*	319	2.5	304-338	18	329	2.7	308-348	17
VOLU	356	2.8	344-367	7	351	3.6	343-363	6
STJO	352	2.6	337-367	13	349	2.3	338-361	13
DUVL	341	2.6	329-355	9	339	2.6	329-354	10
NASS	362	3.8	331-379	13	360	3.2	338-377	13

*Fresh water populations.

TABLE 24. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Head Depth							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	267	1.6	252-296	37	263	1.5	239-286	55
ESCA	281	2.2	270-290	7	276	3.5	262-288	9
OKAL	311	3.8	300-327	8	294	3.9	281-318	8
WALT	297	5.4	281-313	6	282	2.9	277-296	6
GULF	304	2.5	295-321	9	299	2.8	284-325	20
TAYL	316	2.8	302-334	15	313	2.1	301-327	14
LEVY	340	2.9	322-357	15	332	2.8	316-354	16
HERN	329	2.5	318-347	11	323	3.5	294-344	16
PINE-SARA	309	3.5	282-328	14	311	2.8	290-327	16
LEE	311	2.8	290-342	19	299	1.7	286-312	20
FLAM	333	2.9	320-354	11	321	3.4	306-339	11
FDAD*			--		289	3.8	270-311	10
LARG-LMAT	319	3.6	300-331	7	317	3.9	295-336	11
BIGP	332	2.7	313-360	17	326	2.8	305-357	25
PALM*	302	2.8	280-324	23	293	2.1	274-311	25
INDI-SBRE	325	1.5	316-341	20	318	1.8	309-338	18
MERR	326	4.7	288-356	19	307	2.5	281-327	20
HARN*	300	3.2	276-322	18	286	3.2	257-308	17
VOLU	325	2.7	312-335	7	316	4.9	303-333	6
STJO	327	3.4	309-347	12	309	3.0	297-336	13
DUVL	315	2.8	306-327	9	302	2.1	293-312	10
NASS	337	4.1	308-364	3	324	4.6	293-344	13

*Fresh water populations.

TABLE 25. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Snout Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	109	1.4	92-122	35	111	1.2	87-125	51
ESCA	100	1.4	95-106	7	100	1.9	92-110	9
OKAL	117	1.9	113-126	6	110	2.7	98-116	6
WALT	112	2.1	104-119	6	110	1.6	103-115	6
GULF	109	1.4	103-116	9	109	0.8	103-115	20
TAYL	111	1.1	103-119	15	108	1.2	101-117	15
LEVY	116	1.4	109-127	12	117	1.3	111-124	13
HERN	118	0.8	115-123	9	119	1.2	111-126	13
PINE-SARA	112	1.2	100-122	20	114	0.9	108-121	17
LEE	114	1.2	107-127	19	111	1.0	100-118	20
FLAM	115	2.0	106-124	11	113	1.8	104-126	15
FDAD*			--		112	1.4	105-121	11
LARG-LMAT	115	4.4	107-129	5	114	2.6	105-127	9
BIGP	114	1.1	106-122	16	114	1.3	105-130	25
PALM*	112	0.9	102-120	23	114	1.0	105-126	25
INDI-SBRE	121	1.3	107-134	21	119	0.8	110-123	20
MERR	116	2.3	94-134	19	113	1.3	104-124	19
HARN*	110	1.8	95-126	18	110	1.4	102-121	16
VOLU	118	1.4	113-122	7	116	1.9	113-124	6
STJO	119	1.0	113-125	13	115	1.3	106-120	13
DUVL	100	1.0	95-105	9	100	1.2	91-103	10
NASS	117	1.5	104-126	13	117	1.4	108-126	13

*Fresh water populations.

TABLE 26. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Cheek Height							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	84	1.2	70- 99	37	85	0.7	71- 97	56
ESCA	76	1.6	72- 83	7	77	1.0	72- 81	10
OKAL	88	1.4	83- 94	8	85	0.8	81- 88	8
WALT	81	1.2	77- 84	5	80	2.1	73- 88	6
GULF	90	0.9	85- 94	9	90	0.8	82- 95	20
TAYL	85	1.3	77- 95	15	85	1.0	80- 91	15
LEVY	89	1.4	79- 99	15	87	1.0	78- 93	16
HERN	85	1.4	79- 91	10	85	1.3	76- 93	15
PINE-SARA	91	1.3	82-104	20	91	0.7	87- 95	17
LEE	89	1.1	80- 97	19	88	0.7	81- 93	20
FLAM	98	1.4	90-105	11	95	1.1	88-102	15
FDAD*					90	2.2	78-100	11
LARG-LMAT	88	2.3	82- 96	6	88	1.0	81- 92	11
BIGP	93	0.8	87- 98	17	92	0.9	84-103	25
PALM*	94	0.9	85-101	23	91	0.8	85- 98	25
INDI-SBRE	92	1.2	80-100	21	88	0.8	81- 96	20
MERR	89	1.2	80- 99	20	87	0.8	80- 92	20
HARN*	89	1.3	78- 99	18	85	1.2	78- 94	17
VOLU	93	1.3	88- 97	7	90	2.1	84- 96	6
STJO	94	1.0	88-100	13	93	1.4	85-100	13
DUVL	87	2.0	79- 97	9	85	1.0	79- 89	10
NASS	91	1.0	82- 97	13	90	1.1	83- 95	13

*Fresh water populations.

TABLE 27. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Postorbital Head Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	143	0.9	130-154	37	145	0.9	130-155	56
ESCA	144	2.3	135-155	7	150	2.1	136-156	10
OKAL	155	1.2	152-161	8	151	1.4	144-156	8
WALT	147	1.7	141-152	6	144	2.2	134-149	6
GULF	161	2.2	149-170	9	163	1.7	150-182	20
TAYL	155	1.6	140-165	15	154	1.4	145-161	15
LEVY	167	1.0	160-175	15	164	1.7	154-178	16
HERN	155	1.3	148-162	11	154	1.2	145-162	16
PINE-SARA	157	1.8	145-175	20	162	2.1	148-180	17
LEE	161	1.4	148-172	19	158	1.3	145-169	20
FLAM	174	2.0	165-185	11	173	2.1	163-190	15
FDAD*					149	1.9	137-157	11
LARG-LMAT	155	2.3	142-160	7	154	0.6	152-158	11
BIGP	165	1.8	151-179	17	161	1.6	146-177	25
PALM*	148	1.3	136-158	23	147	1.1	138-157	25
INDI-SBRE	178	1.2	168-190	21	175	1.4	161-192	20
MERR	165	2.1	140-178	20	165	2.3	147-183	20
HARN*	140	2.3	125-157	18	145	1.8	130-160	17
VOLU	172	3.1	160-178	7	173	2.2	165-182	6
STJO	173	1.7	162-185	13	175	2.1	162-188	13
DUVL	165	1.3	161-172	9	165	2.1	154-174	10
NASS	180	2.1	167-192	13	178	1.9	165-193	13

*Fresh water populations.

TABLE 28. Proportional Measurements as Thousandths of Standard Length for *Cyprinodon* from Florida.

Population or Location	Interorbital Bony Width							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	90	1.3	76-106	37	87	1.0	72-107	56
ESCA	93	1.9	85-101	7	94	1.7	86-102	10
OKAL	102	2.1	91-107	8	102	1.0	97-105	8
WALT	95	2.3	88-102	6	97	2.0	88-101	6
GULF	104	1.6	97-111	9	107	1.6	95-119	20
TAYL	103	1.0	97-113	15	104	1.1	97-111	15
LEVY	114	1.4	106-123	15	114	1.2	106-123	16
HERN	107	1.2	103-115	11	110	1.3	103-120	16
PINE-SARA	106	1.5	93-118	20	105	1.8	89-118	17
LEE	103	1.5	89-113	19	100	1.2	91-110	20
FLAM	110	2.2	102-124	11	107	1.7	96-119	15
FDAD*			--		96	3.3	79-112	11
LARG-LMAT	103	2.7	92-115	7	96	1.9	83-105	11
BIGP	107	1.5	100-119	17	102	1.0	94-109	25
PALM*	96	1.1	84-104	23	95	1.2	88-114	25
INDI-SBRE	122	1.3	114-134	21	122	1.0	116-134	20
MERR	113	1.5	103-128	20	110	1.3	103-127	20
HARN*	105	1.2	97-117	18	101	1.4	90-109	17
VOLU	114	2.2	106-123	7	112	2.1	104-118	6
STJO	118	1.8	110-130	13	113	1.6	104-126	12
DUVL	117	0.9	113-120	9	114	1.2	107-120	10
NASS	120	1.3	107-127	13	121	1.8	108-131	13

*Fresh water populations.

TABLE 29. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Orbit Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	109	1.0	97-122	37	103	0.7	92-114	56
ESCA	106	1.4	101-111	7	104	1.1	96-108	10
OKAL	100	1.0	95-104	8	101	1.6	92-105	8
WALT	106	2.6	101-116	5	103	2.6	96-113	6
GULF	101	0.9	99-107	9	103	1.3	90-111	20
TAYL	103	0.9	98-109	15	103	0.8	98-109	15
LEVY	108	0.9	102-113	15	106	0.9	101-112	16
HERN	114	1.1	107-120	11	111	1.0	106-120	16
PINE-SARA	106	1.1	97-114	20	100	1.2	91-108	17
LEE	108	0.9	102-115	19	106	0.8	98-113	20
FLAM	109	1.5	102-119	11	111	1.6	103-126	15
FDAD*					113	1.5	105-121	11
LARG-LMAT	111	3.1	98-121	7	114	2.4	106-130	11
BIGP	110	0.7	106-119	17	108	0.9	102-119	25
PALM*	109	1.2	99-121	23	107	0.7	100-115	25
INDI-SBRE	105	0.7	100-112	21	101	0.7	93-106	20
MERR	106	1.2	96-114	20	103	0.8	97-110	20
HARN*	98	1.4	90-114	18	104	1.1	97-115	17
VOLU	98	1.4	94-105	7	97	1.8	91-102	6
STJO	99	0.9	92-106	13	95	1.1	89-102	13
DUVL	91	1.0	87- 96	9	91	1.5	83- 97	10
NASS	101	1.0	95-106	13	100	0.7	95-103	13

*Fresh water populations.

TABLE 30. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Orbit to Angle of Preopercle

Population or Location	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	110	1.1	95-121	37	111	0.7	101-122	56
ESCA	104	1.9	94-111	7	107	1.3	100-113	10
OKAL	122	1.4	118-130	8	116	1.2	110-119	8
WALT	111	0.9	107-113	6	110	2.1	104-117	6
GULF	121	3.1	98-128	9	123	1.2	115-134	20
TAYL	121	1.3	112-130	15	119	1.5	111-130	15
LEVY	126	1.5	117-137	15	123	1.3	116-134	16
HERN	121	1.4	115-130	11	120	1.2	113-129	16
PINE-SARA	124	1.5	115-135	20	123	0.9	116-129	17
LEE	121	1.4	106-135	19	118	1.1	108-128	20
FLAM	134	1.8	123-144	11	131	1.3	123-138	15
FDAD*					119	1.5	109-127	11
LARG-LMAT	116	2.5	107-123	7	119	1.6	112-127	10
BIGP	123	0.9	118-133	17	123	0.9	111-134	25
PALM*	123	1.4	112-135	23	122	1.0	114-132	25
INDI-SBRE	132	1.6	113-146	21	128	1.3	117-137	20
MERR	126	2.0	108-142	20	123	1.3	115-135	20
HARN*	124	1.7	105-132	17	119	1.6	107-131	17
VOLU	129	2.7	122-141	7	129	2.8	120-136	6
STJO	136	2.1	124-145	13	129	1.2	122-137	13
DUVL	131	1.8	121-138	9	124	1.4	118-130	10
NASS	132	1.8	120-144	13	133	1.6	122-140	13

*Fresh water populations.

TABLE 31. Proportional Measurements as Thousandths of Standard Length for Cyprinodon from Florida.

Population or Location	Opercle Length							
	Males				Females			
	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
HUBB*	107	0.9	96-118	37	110	1.0	98-149	56
ESCA	107	2.3	99-133	7	113	1.5	108-121	10
OKAL	116	1.9	109-126	8	113	1.0	108-116	8
WALT	108	1.6	103-113	6	104	1.9	96-109	6
GULF	121	1.8	115-132	9	124	1.2	116-138	20
TAYL	116	1.4	108-131	15	115	1.2	109-124	15
LEVY	125	0.9	121-134	15	125	1.4	115-132	16
HERN	114	1.6	103-121	11	114	0.9	108-120	16
PINE-SARA	119	2.0	107-138	20	122	1.7	111-137	17
LEE	120	1.4	109-131	19	119	1.3	111-135	20
FLAM	129	2.0	116-138	11	131	1.9	122-145	15
FDAD*					107	2.0	97-122	11
LARG-LMAT	117	2.0	107-122	7	116	0.6	112-120	11
BIGP	125	1.7	109-141	17	125	1.4	110-140	25
PALM*	108	1.3	94-116	23	106	1.3	97-121	25
INDI-SBRE	136	1.3	120-146	21	135	1.4	122-149	20
MERR	126	1.8	101-140	20	128	1.9	117-147	20
HARN*	103	1.5	91-116	18	110	1.3	101-120	17
VOLU	132	2.4	125-142	7	133	0.9	129-136	6
STJO	128	1.7	114-140	13	129	1.7	118-137	13
DUVL	125	1.2	120-130	9	126	2.0	116-135	10
NASS	135	2.3	118-148	13	136	1.7	125-148	13

*Fresh water populations.

TABLE 32. Summary of Sexual Dimorphism in Measurements of Florida Cyprinodon.

Character	variegatus	hubbsi
Body Depth	M	–
Body Width	F	F
Caudal Peduncle Depth	M	M
Predorsal Length	F	F
Dorsal Origin to Caudal Base	M	M
Prepectoral Length	–	–
Anal Origin to Caudal Base	M	M
Pectoral Origin to Dorsal Origin	M	–
Pelvic Length	M	M
Head Length	–	–
Head Depth	M	–
Snout Length	–	–
Cheek Height	M	–
Postorbital Head Length	–	–
Interorbital Bony Width	M	–
Orbit Length	M	M
Orbit to Angle of Preopercle	M	–
Opercle Length	–	–

"M" indicates that males have significantly larger means than females, "F" indicates the reverse, and a dash indicates no significant difference between the means. Levels of probability greater than .05 were considered not significant.

TABLE 33. Chemical and Biological Conditions in Oklawaha Lakes (from Brezonik et. al., 1969).

Constituent*	Weir	Harris	Griffin	Eustis	Dora
Diss. O_2	7.60	9.7	8.4	8.78	11.4
Cond.	135	230	290	275	335
pH	7.2	8.8	8.9	8.9	9.5
Alkalinity	15.1	91	112	104	130
COD	25	48	78	112	157
Color	5	13	25	28	43
Secchi Disc	1.2	0.8	0.5	0.6	0.3
Turbidity	3	20	28	25	28
Sus. solids	22	13	27	46	77
TON	0.97	1.7	3.0	4.1	5.3
NH_3-N	0.25	0.19	0.18	0.20	0.17
Ortho PO_4	0.006	0.010	0.014	0.014	0.108
NO_2-N	0.004	0.004	0.007	0.006	0.005
NO_3-N	0.05	0.05	0.09	0.24	0.11
Total P	0.021	0.035	0.20	0.22	0.39
SiO_2	0.34	3.4	0.40	1.4	0.05
Fe (total)	T	0.01	0.01	0.01	0.01
Mn (total)	0.005	0.006	0.003	0.005	0.003
Ca^{+2}	1.4	23.1	28.9	26.3	30.5
Mg^{+2}	3.1	6.1	9.6	10.7	14.2
Na^{+}	15.5	9.7	14.0	14.5	18.1
K^{+}	1.0	0.9	2.1	2.4	3.4
Cl^{-}	26.8	12.8	17.5	18.7	22.3
$SO_{4=}$	4.8	4.9	6.7	7.1	12.3
Chor *a*	8.4	17.7	45.4	33.1	72.1
Prim. prod.	0.011	0.037	0.183	0.274	1.02

*Chemical species in mg/l except as follows: alkalinity in mg/l as $CaCO_3$, nitrogen species in mg N/l, phosphorus species in mg P/l, color in mg/l as Pt. specific conductance in μmho cm^{-1}, Secchi disc visibility in meters, chlorophyll *a* in mg/m^3. Primary production in mg C fixed/l-hr.

TABLE 34. Comparison of Fin-Ray Counts in *Cyprinodon* from Oklawaha Lakes.

Lake	$\bar{X}$	S.E.	Range	N
Dorsal Rays				
Weir	10.80	.12	10-12	20
Harris	11.23	.16	10-12	17
Eustis	11.00	.18	9-12	16
Dora	10.75	.12	10-12	20
Anal Rays				
Weir	9.90	.09	9-11	21
Harris	10.12	.08	10-11	17
Eustis	10.00	.00	10	16
Dora	9.90	.12	9-11	20
Caudal Rays				
Weir	14.57	.18	13-16	21
Harris	14.71	.21	14-16	17
Eustis	14.75	.17	14-16	16
Dora	15.25	.20	14-17	20

TABLE 35. Comparison of Scale Counts in Cyprinodon from Oklawaha Lakes.

Lake	$\bar{X}$	S.E.	Range	N
Lateral Scales				
Weir	24.47	.11	24-25	21
Harris	25.00	.17	24-26	17
Griffin	24.62	.18	24-25	8
Yale	25.20	.20	24-27	10
Eustis	25.19	.19	24-26	16
Dora	24.70	.13	24-26	20
Predorsal Scales				
Weir	10.05	.05	10-11	21
Harris	9.82	.13	9-11	17
Griffin	10.00	.00	10	9
Yale	10.00	.15	9-11	10
Eustis	10.00	.09	9-11	16
Dora	10.00	.07	9-11	20
Dorsal Origin to Belly Mid-line Scales				
Weir	14.80	.17	14-17	20
Harris	15.65	.17	15-17	17
Griffin	15.11	.31	14-16	9
Yale	15.70	.30	14-17	10
Eustis	15.56	.26	14-17	16
Dora	16.55	.25	15-19	20

TABLE 36. Comparison of Scale Counts in Cyprinodon from Oklawaha Lakes.

Lake	$\bar{X}$	S.E.	Range	N
Dorsal Origin to Anal Origin Scales				
Weir	12.00	.10	11-13	21
Harris	12.23	.14	11-13	17
Griffin	12.22	.15	12-13	9
Yale	12.40	.16	12-13	10
Eustis	12.37	.18	11-14	16
Dora	12.20	.16	11-13	20
Dorsal Origin to Pelvic Origin Scales				
Weir	11.09	.12	10-12	21
Harris	11.88	.14	10-13	17
Griffin	12.44	.17	12-13	9
Yale	12.00	.26	11-14	10
Eustis	12.31	.18	11-13	16
Dora	12.05	.15	11-13	20
Belly Scales				
Weir	16.90	.26	14-19	21
Harris	17.65	.35	15-20	17
Griffin	16.44	.29	15-18	9
Yale	19.00	.60	16-22	10
Eustis	17.94	.28	16-20	16
Dora	20.55	.44	18-26	20

TABLE 37. Comparison of Scale Counts in Cyprinodon from Oklawaha Lakes.

Lake	$\bar{X}$	S.E.	Range	N
Suborbital Scales				
Weir	7.76	.19	6- 9	21
Harris	7.82	.23	7-10	17
Eustis	8.37	.20	7-10	16
Dora	7.65	.23	5-10	20
Circumference Scales				
Weir	26.43	.31	25-30	21
Harris	28.18	.36	25-30	17
Griffin	27.89	.42	26-30	9
Yale	28.60	.50	26-31	10
Eustis	29.06	.51	26-33	16
Dora	29.50	.47	26-34	20

TABLE 38. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Standard Length (mm)							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	28.8		26.6-33.4	11	31.0		28.6-33.2	21
Harris	29.7		27.1-32.4	8	31.5		29.4-32.5	9
Eustis	28.7		26.6-32.2	6	28.7		26.9-32.1	10
Dora	34.1		31.3-40.2	12	31.4		29.1-36.3	13
	Body Depth							
Weir	328	4.2	308-353	11	325	3.1	301-357	21
Harris	345	7.6	310-376	8	333	4.5	313-353	9
Eustis	346	7.0	319-363	6	354	4.0	324-372	10
Dora	377	2.8	358-396	12	380	3.1	362-408	13
	Body Width							
Weir	194	1.8	183-205	11	212	3.6	193-247	21
Harris	188	2.9	176-197	8	213	4.9	187-238	9
Eustis	188	1.8	183-196	6	233	2.9	219-252	10
Dora	215	1.8	206-230	12	238	2.0	226-249	13

TABLE 39. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Caudal Peduncle Depth							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	172	1.9	161-184	11	162	1.3	149-171	21
Harris	185	3.2	173-199	8	167	1.7	155-172	9
Eustis	186	2.2	179-193	6	180	2.0	173-190	10
Dora	188	1.6	179-196	12	179	1.6	168-188	13
	Predorsal Length							
Weir	528	3.1	505-541	11	549	2.1	534-565	21
Harris	518	3.0	507-531	8	528	3.4	518-544	9
Eustis	509	6.5	489-530	6	532	4.7	511-555	10
Dora	544	2.8	527-555	12	556	2.7	537-570	13
	Dorsal Origin to Caudal Base							
Weir	520	3.4	505-538	11	502	2.0	489-524	21
Harris	547	4.2	531-565	8	528	5.1	497-551	9
Eustis	555	4.0	538-563	6	532	3.8	517-559	10
Dora	538	3.2	517-563	12	524	3.4	507-550	13

TABLE 40. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Prepectoral Length							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	356	2.6	341-372	11	357	1.9	335-371	21
Harris	357	6.1	334-380	8	343	4.0	323-359	9
Eustis	357	3.2	345-367	6	368	4.2	345-387	10
Dora	350	1.9	342-361	12	352	2.3	339-364	13
	Anal Origin to Caudal Base							
Weir	382	2.1	374-395	11	342	2.2	326-365	21
Harris	389	1.9	379-397	8	353	3.6	329-366	9
Eustis	382	3.5	370-391	6	346	2.5	336-363	10
Dora	384	2.4	370-395	12	353	2.1	339-366	13
	Pectoral Origin to Dorsal Origin							
Weir	313	1.7	300-319	11	320	2.4	299-348	21
Harris	307	6.5	280-328	8	320	2.4	309-332	9
Eustis	307	6.3	278-323	6	327	2.3	314-338	10
Dora	350	3.4	327-367	12	354	4.0	326-372	13

TABLE 41. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

Pelvic Length

Lake	Males $\bar{X}$	S.E.	Range	N	Females $\bar{X}$	S.E.	Range	N
Weir	132	2.1	123-147	11	130	1.4	122-139	21
Harris	136	2.0	130-148	8	124	2.2	113-132	9
Eustis	135	1.5	130-139	6	124	2.1	118-138	9
Dora	138	1.2	129-144	12	130	1.1	124-134	13

Head Length

Weir	328	1.9	314-335	11	326	1.9	308-340	21
Harris	325	4.0	303-343	8	311	2.3	301-326	9
Eustis	316	2.5	307-323	6	325	2.7	308-335	10
Dora	327	2.1	319-340	12	327	1.4	317-337	13

Head Depth

Weir	261	1.7	252-270	11	261	1.5	250-270	20
Harris	264	2.8	255-277	8	252	3.0	239-267	9
Eustis	263	2.9	252-273	6	273	2.3	261-286	10
Dora	275	2.8	264-296	12	270	1.5	259-278	13

TABLE 42. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Snout Length							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	110	1.2	102-115	11	112	1.2	102-122	21
Harris	105	4.0	93-122	7	98	2.3	87-106	9
Eustis	100	2.8	92-110	6	116	2.5	110-124	5
Dora	115	0.9	109-118	11	117	0.9	113-125	13
	Cheek Height							
Weir	84	1.5	75- 92	11	86	1.0	75- 96	21
Harris	81	1.5	74- 86	8	78	1.6	71- 87	9
Eustis	75	1.5	70- 80	6	84	1.1	78- 90	10
Dora	91	1.1	85- 99	12	88	1.1	81- 97	13
	Postorbital Head Length							
Weir	145	1.8	136-154	11	144	1.2	135-154	21
Harris	140	2.1	130-148	8	137	1.4	130-146	9
Eustis	139	1.1	135-143	6	147	1.6	137-155	10
Dora	144	1.3	136-152	12	150	1.0	144-155	13

TABLE 43. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Interorbital Bony Width							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	88	1.5	78- 96	11	89	1.1	77- 99	21
Harris	84	1.0	80- 89	8	81	1.6	74- 87	9
Eustis	84	2.5	76- 93	6	83	1.7	72- 88	10
Dora	99	1.2	92-106	12	96	1.3	91-107	13
	Orbit Length							
Weir	114	1.3	106-120	11	108	0.7	102-113	21
Harris	110	2.6	99-122	8	100	1.2	96-106	9
Eustis	104	2.1	97-110	6	104	1.7	92-114	10
Dora	106	1.2	100-115	12	98	0.8	94-103	13

TABLE 44. Proportional Measurements, Expressed as Thousandths of Standard Length, for Cyprinodon from Oklawaha Lakes.

	Orbit to Angle of Preopercle							
	Males				Females			
Lake	$\bar{X}$	S.E.	Range	N	$\bar{X}$	S.E.	Range	N
Weir	111	1.6	99-119	11	113	1.0	106-122	21
Harris	108	1.4	103-115	8	104	0.6	101-106	9
Eustis	102	2.1	95-107	6	111	1.1	106-117	10
Dora	115	1.3	108-121	12	115	1.2	106-121	13
	Opercle Length							
Weir	105	2.0	96-114	8	111	2.3	99-149	21
Harris	110	1.4	102-118	11	104	0.9	100-109	9
Eustis	103	1.4	99-107	6	112	1.4	106-120	10
Dora	109	1.2	103-117	12	113	0.8	108-117	13

LITERATURE CITED

Ager, L. L. 1971. The fishes of Lake Okeechobee, Florida. Quart. J. Fla. Acad. Sci. 34(1):53-62.

Alt, D., and H. K. Brooks. 1965. Age of the Florida marine terraces. J. Geol. 73:406-411.

Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from Escambia River, Alabama and Florida, with ecological and taxonomic notes. Proc. Acad. Natur. Sci. Phila. 106:109-164.

Baird, S. F., and C. Girard. 1853. Description of species of fishes, collected by Captains R. B. Marcy, and Geo. B. McClellan, in Arkansas. Proc. Acad. Natur. Sci. Phila. 6:390-392.

Barlow, G. W. 1958a. Daily movements of desert pupfish, Cyprinodon macularius, in shore pools of the Salton Sea, California. Ecology 39:580-587.

Barlow, G. W. 1958b. High salinity mortality of desert pupfish, Cyprinodon macularius. Copeia 1958(3):231-232.

Barlow, G. W. 1961a. Causes and significance of morphological variation in fishes. Syst. Zool. 10(3):105-117.

Barlow, G. W. 1961b. Social behavior of the desert pupfish, Cyprinodon macularius, in the field and in the aquarium. Amer. Midl. Natur. 65(2):339-359.

Beckham, E. C., and M. F. Mettee, Jr. 1974. Species associations and local distribution of Cyprinodon variegatus Lacepede along the Northern Gulf Coast. Bull. Ass. Southeastern Biol. 21(2):211.

Bohlke, J. E., and C. C. G. Chaplin. 1970. Fishes of the Bahamas and adjacent tropical waters. Livingston Pub. Co., Wynnewood, Pa. 771 pp.

Breder, C. M., Jr. 1932. An annotated list of fishes from Lake Forsythe, Andros Island, Bahamas, with description of three new forms. Amer. Mus. Novitates 551:1-7.

Breder, C. M. Jr. 1934. Ecology of an oceanic fresh water lake, Andros Island, Bahamas, with special reference to its fishes. Zoologic 18(3):57-88.

Brezonik, P. L., W. H. Morgan, E. E. Shannon, and H. D. Putnam. Eutrophication factors in North Central Florida lakes. Fla. Eng. and Ind. Exp. Sta., Univ. Fla. Bull. Ser. No. 134, Water Resour. Res. Center Pub. No. 5.

Briggs, J. C. 1958. A list of Florida fishes and their distribution. Bull. Fla. St. Mus. 2(8):223-318.

Brown, D. W., W. E. Kenner, J. W. Crooks, and J. B. Foster. 1962. Water resources of Brevard County, Florida. Fla. Geol. Surv., Rep. of Invest. No. 28.

Brown, J. H. and C. R. Feldmeth. 1971. Evolution in constant and fluctuating environments: thermal tolerances of desert pupfish (Cyprinodon). Evolution 25(2):390-398.

Carr, A. F. 1936a. A new species of Cyprinodon from Lake Eustis, Florida. Copeia 1936(3):160-163.

Carr, A. F. 1936b. A key to the fresh-water fishes of Florida. Quart. J. Fla. Acad. Sci. 1(1):72-86.

Carr, A., and C. J. Goin. 1955. Guide to the Reptiles, Amphibians, and Freshwater Fishes of Florida. Univ. Fla. Press, Gainesville, Fla. 341 pp.

Chipman, R. K. 1958. Morphological variation of Cyprinodon variegatus (Cyprinodontidae) correlated with salinity of habitat. M.S. Thesis. Tulane Univ., New Orleans, Louisiana.

Christensen, R. F. 1965. An ichthyological survey of Jupiter Inlet and Loxahatchee River, Florida. M. S. Thesis, Fla. St. Univ., Tallahassee, Fla.

Coker, R. E. 1962. This Great and Wide Sea. Univ. of North Carolina Press, Harper and Brothers, N.Y. 325 pp.

Cooke, C. W. 1939. Scenery of Florida. Bull. Fla. Geol. Surv. No. 17:1-118.

Cooke, C. W. 1945. Geology of Florida. Bull. Fla. Geol. Surv. No. 29:1-399.

Cowles, R. B. 1934. Notes on the ecology and breeding habits of the desert minnow Cyprinodon macularius. Copeia 1934(1):40-42.

Duellman, W. E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bull. Fla. St. Mus. 3:181-324.

Echelle, A. A. 1973. Behavior of the pupfish, Cyprinodon rubrofluviatilis. Copeia 1973(1):68-76.

Echelle, A. A., A. F. Echelle, and L. G. Hill. 1972. Interspecific interactions and limiting factors of abundance and distribution in the Red River pupfish, Cyprinodon rubrofluviatilis. Amer. Midl. Natur. 88(1):109-130.

Echelle, A. A., C. Hubbs, and A. F. Echelle. 1972. Developmental rates and tolerances of the Red River pupfish, Cyprinodon rubrofluviatilis. Southwestern Natur. 17(1):55-60.

Fanara, D. M. 1964. Notes on the biology of a salt marsh minnow, Cyprinodon variegatus. Proc. 51st Annu. Mtg. N.J. Mosquito Exterm. Ass. 152-159.

Foster, N. R. 1967. Comparative studies on the biology of killifish (Pisces, Cyprinodontidae). Ph.D. Thesis. Cornell Univ. (Libr. Congr. Card No. Mic. 67-8759). 354 pp. University Microfilms, Ann Arbor, Mich.

Fowler, H. W. 1906. Some cold-blooded vertebrates of the Florida Keys. Proc. Acad. Natur. Sci. Phila. 58:77-113.

Fowler, H. W. 1939. Notes on fishes from Jamaica with descriptions of three new species. Notulae Naturae 35:1-16.

Gilbert, C. R., and R. M. Bailey. 1972. Systematics and zoogeography of the American cyprinid fish Notropis (Opsopoeodus) emiliae. Occ. Pap., Mus. Zool. Univ. Mich. No. 664:1-35.

Gilmore, R. G., Jr., and L. D. Williams. (unpublished manuscript). Cyprinodon variegatus (Lacepede, 1803): Morphological variation in eastern Florida populations with notes on Cyprinodon laciniatus Hubbs and Miller, 1942, from the Bahamas.

Gore, R. H. 1972. Zoogeographical aspects of decapod crustacea in the Indian River region of Florida. Amer. Zool. 12(4):509.

Gosline, A. 1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus Fundulus. Occ. Pap., Mus. Zool. Univ. Mich. 519:1-17.

Greenfield, D. W., and R. B. Grinols. 1965. Cyprinodon variegatus on the Olympic peninsula, Washington. Copeia 1965(1):115-116.

Gunter, G. 1941. Death of fishes due to cold on the Texas coast, January 1940. Ecology 22(2):203-208.

Gunter, G. 1945. Studies on marine fishes of Texas. Pub. Inst. Mar. Sci., Univ. of Texas 1(1):1-190.

Gunter, G. 1950. Distributions and abundance of fishes on the Aransas National Wildlife Refuge, with life history notes. Pub. Inst. Mar. Sci., Univ. of Texas. 1(2):89-101.

Gunter, G. 1956. Some relations of faunal distributions to salinity in estuarine waters. Ecology 37(3):616-619.

Gunter, G. 1967. Vertebrates in hypersaline waters. Contrib. in Mar. Sci. 12:230-241.

Gunter, G., and G. E. Hall. 1963. Biological investigations of the St. Lucie estuary (Florida) in connection with Lake Okeechobee discharges through the St. Lucie Canal. Gulf Res. Rep. 1(5):189-307.

Gunter, G., and G. E. Hall. 1965. A biological investigation of the Caloosahatchee estuary of Florida. Gulf Res. Rep. 2(1):1-71.

Harrington, R. W., and E. S. Harrington. 1961. Food selection among fishes invading a high subtropical salt marsh; from onset of flooding through the progress of a mosquito brood. Ecology 42:646-665.

Hellman, R. E. 1954. Further extensions of the range of the sheepshead killifish, Cyprinodon hubbsi Carr. Quart. J. Fla. Acad. Sci. 16(3):198.

Herald, E. S., and R. S. Strickland. 1949. An annotated list of fishes of Homosassa Springs, Florida. Quart. J. Fla. Acad. Sci. 11(4):99-109.

Hildebrand, S. F. 1917. Notes on the life history of the minnows Gambusia affinis and Cyprinodon variegatus. Annu. Rep. U.S. Comm. Fish., Doc. No. 857, App. 6:3-15.

Hildebrand, S. F., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1):1-366.

Hill, L. G., and J. P. Holland. 1971. Preference behavior of the Red River pupfish, Cyprinodon rubrofluviatilis (Cyprinodontidae), to acclimation-salinities. Southwestern Natur. 16(1):55-63.

Hoedeman, J. J. 1958. The frontal scalation pattern in some groups of tooth carps (Pisces-Cyprinodontiforms). Bull. Aquatic Biol. 1(3):23-28.

Hubbs, C. L. 1936. Fishes of the Yucatan Peninsula. Carnegie Inst. Wash., Publ. 457:157-287.

Hubbs, C. L., L. C. Hubbs, and R. E. Johnson. 1943. Hybridization in nature between species of Catostomid fishes. Contrib. Lab. Vert. Biol. 22:1-76.

Hubbs, C. L., and K. F. Lagler. 1958. Fishes of the Great Lakes region. Rev. ed., Bull. Cranbrook Inst. Sci. 26:1-213.

Hubbs, C. L., and R. R. Miller. 1942. Studies of the fishes of the order Cyprinodontes. XVIII. Cyprinodon laciniatus, new species, from the Bahamas. Oc. Pap., Mus. Zool. Univ. Mich. 458:1-11.

Hubbs, C., and G. E. Drewry. 1959. Survival of hybrids between cyprinodont fishes, with a discussion of the correlation between hybridization and phylogenetic relationships. Publ. Inst. Mar. Sci., Univ. of Texas. 6:81-91.

Johnson, R. I. 1972. The Unionidae (Mollusca:Bivalvia) of peninsular Florida. Bull. Fla. St. Mus. 16(4):181-247.

Johnson, R. I. 1973. Distribution of Hydrobiidae, a family of fresh and brackish water gastropods in peninsular Florida. Occ. Pap. on Mollusks. 3(46):281-303.

Joseph, E. B., and R. W. Yerger. 1956. The fishes of Alligator Harbor, Florida, with notes on their natural history. Fla. St. Univ. Stud. 22:111-156.

Jordan, D. S. 1884. List of fishes collected at Key West, Florida, with notes and descriptions. Proc. U.S. Nat. Mus. 7:103-150.

Jordan, D. S., and C. H. Gilbert. 1883. Synopsis of fishes of North America. Bull. U.S. Nat. Mus. 16:1-1018.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus. 1(47):1-3313.

Kaill, W. M. 1968. Ecology and behavior of Cyprinodontid fishes: Jordanella floridae, Floridichthys carpio, Cyprinodon variegatus. Ph.D. Thesis. Cornell Univ. (Libr. Congr. Card No. Mic. 68-3508). 159 pp. University Microfilms, Ann Arbor, Mich.

Kilby, J.D. 1955. The fishes of two Gulf coastal marsh areas of Florida. Tulane Stud. Zool. 2(8):176-247.

Kilby, J. D., and D. K. Caldwell. 1955. A list of fishes from the southern tip of the Florida peninsula. Quart. J. Fla. Acad. Sci. 18(3):195-206.

Kinne, O. 1966. Physiological aspects of animal life in estuaries with special reference to salinity. Netherlands Sea Res. 3(2):222-244.

Kinne, O., and E. M. Kinne. 1962a. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. Canad. J. Zool. 40:231-253.

Kinne, O., and E. M. Kinne. 1962b. Effects of salinity and oxygen in developmental rates in a cyprinodont fish. Nature 193:1097-1098.

LaBounty, J. F. 1968. Some ecological and taxonomic considerations of Death Valley cyprinodonts. M.S. Thesis. Univ. of Nevada, Las Vegas.

LaBounty, J. F., and J. E. Deacon. 1972. Cyprinodon milleri, a new species of pupfish (family Cyprinodontidae) from Death Valley, California. Copeia 1972(4):769-780.

Liu, R. K. 1965. Evolution of male courtship behavior in fishes of the genus Cyprinodon. Amer. Zool. 5:685-686.

Liu, R. K. 1969. The comparative behavior of allopatric species (Teleostei-Cyprinodontidae:Cyprinodon). Ph.D. Thesis. Univ. of Calif. (Los Angeles). (Libr. Congr. Card No. Mic. 70-8234). 185 pp. University Microfilms, Ann Arbor, Mich.

MacNeil, F. S. 1949. Pleistocene shorelines in Florida and Georgia. U.S. Geol. Surv. Prof. Pap. 221-F:95-107.

McLane, W. M. 1955. The fishes of the St. Johns River system. Ph.D. Thesis. Univ. of Fla. (Libr. Congr. Card No. 59-3559). 362 pp. University Microfilms, Ann Arbor, Mich.

McNulty, J. K., W. N. Lindal, Jr., and J. E. Sykes. 1972. Cooperative Gulf of Mexico estuarine inventory and study, Florida: Phase I, area description. Nat. Ocean. Atmospheric Admin. Technical Rep. NMFS Circ.-368.

Martin, F. D. 1967. Osmotic shock survival in certain cyprinodont fishes. M.A. Thesis, Univ. of Texas, Austin.

Martin, F. D. 1968. Intraspecific variation in osmotic abilities of Cyprinodon variegatus Lacepede. Ecology 49(6):1186-1188.

Martin, F. D. 1969. Some factors influencing penetration into rivers by fishes of the genus Cyprinodon. Ph.D. Thesis. Univ. of Texas, Austin. (Libr. Congr. Card No. 69-6181). 92 pp. University Microfilms, Ann Arbor, Mich.

Martin, F. D. 1970. Feeding habits of Cyprinodon variegatus (Cyprinodontidae) from the Texas coast. Southwestern Natur. 14:368-369.

Martin, F. D. 1972. Factors influencing local distribution of Cyprinodon variegatus (Pisces: Cyprinodontidae). Trans. Amer. Fish. Soc. 101(1):89-93.

Miller, R. R. 1943a. The status of Cyprinodon macularius and Cyprinodon nevadensis, two desert fishes of Western North America. Occ. Pap., Mus. Zool. Univ. Mich. 473:1-25.

Miller, R. R. 1943b. Cyprinodon salinus, a new species of fish from Death Valley, California. Copeia 1943(2):69-78.

Miller, R. R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool., Univ. Mich. 68:1-155.

Miller, R. R. 1950. Speciation in fishes of the genera Cyprinodon and Empetrichthys, inhabiting the Death Valley region. Evolution 4(2):155-163.

Miller, R. R. 1962. Taxonomic status of Cyprinodon baconi, a killifish from Andros Island, Bahamas. Copeia 1962(4):836-837.

Moore, G. A. 1968. Fishes, p. 22-165. In W. F. Blair, A. P. Blair, P. Brodkorb, F. R. Cagle, G. A. Moore; Vertebrates of the United States. 2nd ed. McGraw-Hill Book Co., New York, N.Y. 616 pp.

Myers, G. S. 1935. An annotated list of the cyprinodont fishes of Hispaniola, with description of two new species. Zoologica 10:301-316.

Myers, G. S. 1937. Fresh-water fishes and West Indian Zoogeography. Smithsonian Rep. 1937:339-364.

Naiman, R. J., S. D. Gerking, and T. D. Ratcliff. 1973. Thermal environment of a Death Valley pupfish. Copeia 1974(2):366-369.

Neill, W. T. 1957. Historical biogeography of present-day Florida. Bull. Fla. St. Mus., Biol. Sci. 2(7):175-220.

Odum, H. T. 1953. Factors controlling marine invasion into Florida fresh water. Bull. Mar. Sci. Gulf and Caribbean 3:134-156.

Otto, R. G., and S. D. Gerking. 1973. Heat tolerance of a Death Valley pupfish (genus Cyprinodon). Physiol. Zool. 46(1):43-49.

Raney, E. C., R. H. Backus, R. W. Crawford, and C. R. Robbins. 1953. Reproductive behavior in Cyprinodon variegatus Lacepede, in Florida. Zoologica 38(2):97-104.

Reid, G. K. 1948. Extension of the range of the sheepshead killifish, Cyprinodon hubbsi Carr. Quart. J. Fla. Acad. Sci. 11(2-3):67-68.

Renfro, J. L., and L. G. Hill. 1971. Osmotic acclimation in the Red River pupfish, Cyprinodon rubrofluviatilis. Biochem. Physiol. 40A:711-714.

Renfro, J. L., and L. G. Hill. 1972. Cytological adaptations in the gills of the Red River pupfish, Cyprinodon rubrofluviatilis. Southwestern Natur. 17(2):197-216.

Renfro, W. C. 1959. Survival and migration of fresh-water fishes in salt water. Tex. J. Sci. 11:172-180.

Renfro, W. C. 1960. Salinity relations of some fishes in the Aransas River, Texas. Tulane Stud. Zool. 8(3):83-91.

Rinckey, G. R., and C. H. Saloman. 1964. Effect of reduced water temperature on fishes of Tampa Bay, Florida. Quart. J. Fla. Acad. Sci. 27(1):9-16.

Simpson, D. G., and G. Gunter. 1956. Notes on habits, systematic characters and life histories of Texas salt water cyprinodonts. Tulane Stud. Zool. 4:115-134.

Springer, V. G., and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Fla. St. Bd. Conserv. Mar. Lab., Prof. Pap. Ser. 1:1-104.

Stevenson, M. M., and T. M. Buchanan. 1973. An analysis of hybridization between the cyprinodont fishes Cyprinodon variegatus and C. elegans. Copeia 1973(4):682-691.

Strawn, K. and J. E. Dunn. 1967. Resistance of Texas salt and freshwater marsh fishes to heat death at various salinities. Texas J. Sci. 19(1):57-76.

Sweet, J. G., and O. Kinne. 1964. The effects of various temperature-salinity combinations on the body form of newly hatched Cyprinodon macularius (Teleostei). Helgol. Wiss. Meersunters. 11(2):49-69.

Tabb, D. C., and R. B. Manning. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957, through September, 1960. Bull. Mar. Sci. Gulf and Caribbean 11(4):552-649.

Tagatz, M. E. 1967. Fishes of the St. Johns River. Quart. J. Fla. Acad. Sci. 30(1):25-50.

Thompson, F. G. 1968. The aquatic snails of the family Hydrobiidae of peninsular Florida. Univ. of Fla. Press, Gainesville, pp. i-xv, 1-268, 69 figs.

Vandermeer, J. H. 1966. Statistical analysis of geographic variation of the fathead minnow, Pimephales promelas. Copeia 1966(3): 457-466.

Vernon, R. O. 1951. Geology of Citrus and Levy Counties, Florida. Bull. Fla. Geol. Surv. No. 33:1-256.

Wales, J. H. 1930. Biometrical studies of some races of cyprinodont fishes, from Death Valley region, with description of Cyprinodon diabolis, n. sp. Copeia 1930(3):61-70.

Warlen, S. M. 1964. Some aspects of the life history of Cyprinodon variegatus in southern Delaware. M.S. Thesis, Univ. Delaware, Newark.

White, W. A. 1958. Some geomorphic features of central peninsular Florida. Bull. Fla. Geol. Surv. No. 41:1-92.

White, W. A. 1972. The geomorphology of the Florida Peninsula. Fla. Bur. Geol., Geol. Bull. 51:1-164.

Work, R. C. 1969. Systematics, ecology, and distribution of the mollusks of Los Roques, Venezuela. Bull. Mar. Sci. 19(30): 614-711

Wyrick, G. G. 1960. The ground-water resources of Volusia County, Florida. Fla. Geol. Surv., Rep. of Invest. No. 22:1-132.